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Seattle, Washington

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SCIENTIFIC EDITOR, *Fishery Bulletin*

Dr. Andrew E. Dizon
Southwest Fisheries Center La Jolla Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, CA 92038

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MORPHOMETRIC VARIATION OF PACIFIC OCEAN PERCH, *SEBASTES ALUTUS*, OFF WESTERN NORTH AMERICA

JAY C. QUAST[1]

ABSTRACT

Pacific ocean perch, *Sebastes alutus*, vary in body form over the eastern Pacific Ocean and southeastern Bering Sea. When related to a 260 mm standard length, a small adult size, most of 18 body measurements change from east to west as V-shaped clines. Belly size, however, lengthens as a single cline from the Vancouver vicinity westward, and the lengthening is coupled with shortening of measurements complementary to the belly measurement, from head to belly and belly to tail. Most adult body dimensions are sexually dimorphic, but the dimorphism is slight. Growth inflections may occur but, if so, are hidden in the data. Body form does not change markedly with growth except for the symphyseal knob, which becomes relatively larger, and the 3d anal-fin spine, which becomes relatively shorter. Putative subspecies of *S. alutus* probably are premature because supportive morphometric comparisons and criteria on the subspecies seem based on too few data, and do not adequately consider complex clinal variation and growth allometry evidenced in the eastern part of the species range. Also, significant morphometric variation may be phenotypic.

Pacific ocean perch, *Sebastes alutus*, a commercially important rockfish (Scorpaenidae) in the North Pacific Ocean, range from northern Honshu, Japan, to California. To date, the species' taxonomy has been based on relatively limited local representation, on preserved material, and on analyses without probabilistic interpretation or attention to allometric growth. Matsubara (1943) identified a Honshu representative as a new species (*Sebastes paucispinosus*), but Barsukov (1964), after examining specimens taken across the North Pacific Ocean, suggested that the variation he found indicated, at most, possible eastern and western Pacific subspecies, with both possibly occurring off the Aleutian Arc. Chen (1971) demonstrated that growth rate, can influence body proportions in a *Sebastes* species, and Westrheim (1973) found a cline of increasing growth rate in *S. alutus* from the northern Gulf of Alaska to Washington (Quast[2] found that the cline may be more related to latitude than temperature).

Because of the commercial importance of Pacific ocean perch and the lack of definitive information on possible subspecies or genetic stocks at the onset of the study, the National Marine Fisheries Service gathered morphometric data on representatives from the Gulf of Alaska and eastern Bering Sea from 1968 to the mid-1970's. We sought evidence of disjunct geographic variation that might indicate genetic stocks, and analyzed for characteristics of growth and sexual variation of possible taxonomic significance. Sampling was in the shallow range of the species distribution, at <200 fathoms (366 m).

METHODS

The prohibitively large volume needed for specimen storage for an extensive statistical study and the shrinkage, bending, and other distortions caused by preservation were avoided by photographing freshly trawled Pacific ocean perch. A portable stand supported a 35 mm camera and flash unit 145 cm above a V-shaped easel, which helped restrain the fish from vessel motion. The long focal distance minimized foreshortening in the photographs, and a 100 mm telephoto lens reduced field size to include only the specimen, a centimeter scale, a numbered theater ticket, and a plastic card with pencil-inscribed catch information. Specimens were flattened, straightened, and centered on the easel; fins were placed as erect as possible; and the lower jaw was propped closed with handheld forceps. Later, in the laboratory, body measurements were taken from images projected from the color transparencies onto the back of a ground-glass screen. The images

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821; present address: 1565 Jamestown Street S.E., Salem, OR 97302.

[2]Jay C. Quast. Annual growth in Pacific ocean perch, *Sebastes alutus*: variation, stanzas, compensation, and simulation. Manuscr. in prep.

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were brought to natural size by reference to the centimeter scale in each photograph. Accuracy was ensured for body-depth measurements by using a right-angle scale on the body axis.

The study used 18 linear measurements[3] (nearest millimeter) in addition to standard length (SL) of approximately 1,500 specimens sampled from the Bering Sea and Gulf of Alaska during summers of 1968-70 (Fig. 1, Table 1). The measurements gave major dimensions of the body and accessory structures, similar to those standard in taxonomic studies (Hubbs and Lagler 1949):

Standard length.—From tip of the premaxillary to the skin deflection (evidenced by a change in shading) at end of the hypural plate.

Nape.—From tip of premaxillary to the anterior insertion (junction of anterior outline with body profile) of the first spinous ray in the dorsal fin.

Spinous dorsal-fin length.—From anterior insertion of the spinous dorsal fin to the posterior insertion (junction of posterior outline of spine with body profile) of the 13th spinous fin ray.

Hind-trunk dorsal.—From posterior insertion of the 13th spinous fin ray to end of the hypural plate.

Hind-trunk ventral.—From posterior insertion of the second anal-fin spine to end of the hypural plate.

Belly.—From posterior insertion of the pelvic fin to posterior insertion of second anal-fin spine.

Pelvic insertion.—From tip of the premaxillary to posterior insertion of the pelvic fin.

Head.—From tip of the premaxillary to posterior edge of the opercular flap.

Body-depth pelvic.—Dorsoventral distance, taken perpendicular to the longitudinal axis of the fish, from the posterior insertion of pelvic fin to dorsal body outline.

Body-depth anal.—Dorsoventral distance, taken perpendicular to the longitudinal axis of the fish, from the anterior insertion of first anal spine to dorsal body outline.

Caudal peduncle.—Shortest distance across caudal peduncle, taken perpendicular to its longitudinal axis.

Orbit.—Greatest diameter between opposite sides of the orbit, taken parallel to longitudinal axis

[3]Data for the measurements, including additional measurements not given in this paper, are available on tape as JQUAST/MORF1 on file at the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, 2725 Montlake Blvd. East, Seattle, WA 98112.

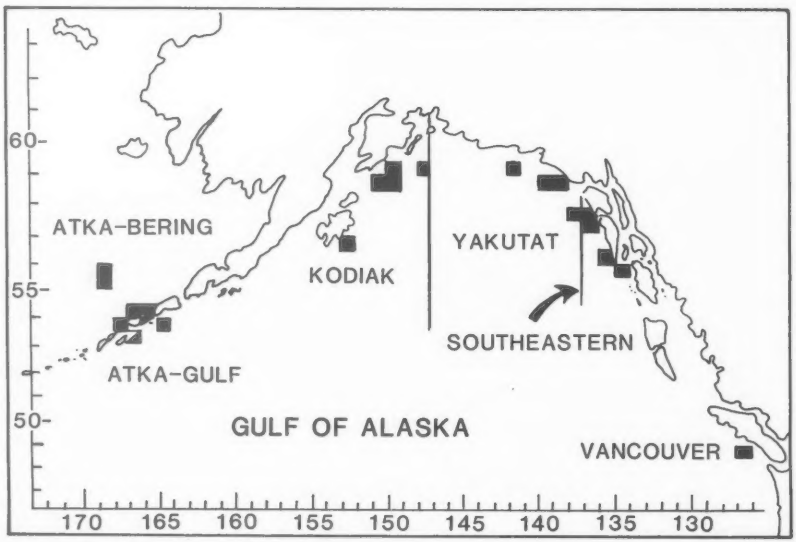

FIGURE 1.—Geographic regions and statistical areas (dark rectangles) where Pacific ocean perch were obtained for this study.

TABLE 1.—Standard-length (SL) frequencies of Pacific ocean perch used in this study. Geographic zones are shown in Figure 1. M = male; F = female.

Standard length (mm)		Atka-Bering		Atka-Gulf		Kodiak		Yakutat		Southeastern		Vancouver	
Class	Midpoint	M	F	M	F	M	F	M	F	M	F	M	F
115-134	125.5	5	5	—	—	—	—	—	—	—	1	—	—
135-154	145.5	3	4	—	1	—	—	—	—	—	1	—	—
155-174	165.5	4	5	1	—	4	4	—	—	1	2	—	—
175-194	185.5	16	14	2	4	14	15	2	5	4	5	—	—
195-214	205.5	20	15	13	9	6	7	4	11	15	7	—	—
215-234	225.5	13	26	51	55	10	6	16	24	13	8	—	—
235-254	245.5	36	22	49	52	6	7	14	19	7	5	5	—
255-274	265.5	22	19	25	12	7	8	9	10	12	17	4	2
275-294	285.5	16	22	15	13	19	9	4	10	16	9	10	4
295-314	305.5	10	13	26	21	65	33	6	7	23	5	13	3
315-334	325.5	17	25	13	22	16	35	4	8	11	5	9	4
335-354	345.5	3	26	1	7	4	18	4	4	—	—	2	8
355-374	365.5	3	17	—	1	—	2	1	5	—	1	2	1
375-394	385.5	—	2	—	—	—	—	2	—	1	—	—	1
395-414	405.5	—	—	—	—	—	—	—	—	1	—	—	1
Total by sex:		168	215	196	197	151	144	66	103	104	66	45	24
Region totals:		383		393		295		169		170		69	
Average SL, by region:		260.5		257.9		281.4		261.5		261.2		308.4	
Average SL, all data[1]:		266.41 (N = 1,479)											

[1]Class midpoints weighted by frequency.

of the fish.

Longest pectoral-fin ray.—From tip of the longest ray to its origin.

Upper-jaw length.—Greatest distance from tip of the premaxillary to posterior edge of the maxillary.

Upper-jaw width.—Greatest width of this part taken perpendicular to axis of the mouth line in a closed mouth.

Symphyseal knob.—From tip of symphyseal knob to its posterior insertion.

6th dorsal spinous fin ray.—From tip of this fin ray to its posterior insertion.

13th spinous ray in dorsal fin.—From tip of this ray to its posterior insertion.

3d anal-fin spine.—From tip of this spine to its posterior insertion.

The data were divided into six geographic regions (Atka-Bering, Atka-Gulf, Kodiak, Yakutat, Southeastern, and Vancouver (Fig. 1)), and measurements regressed on SL by sex after all variates were $\log_{10}$ transformed. (Transformation allowed measurements to be expressed as linear functions of SL and stabilized the variance.) Geographic and sexual variation were tested by analysis of covariance (ANCOVA), with statistical tests "significant" when $P \leq 0.05$.

In "allometric" growth in fishes, the size of one variate bears a power relationship to an index of body length. The power exponent can be expressed as the slope of a simple linear regression fit to log-transformed variates, the "allometric equation", as used in this study. A slope greater than unity, "positive allometry" (Simpson et al. 1960), indicates that growth in a body dimension relative to growth in fish length (SL in the present paper) increases as fish length increases; a slope less than unity, "negative allometry", indicates that growth in a body dimension decreases; and a slope of unity, "isometry", indicates that it stays the same.

A preliminary survey of the measurement data disclosed that most body dimensions probably grow allometrically, although not strongly so because slopes are near unity (Table 2). Because body proportions that relate size of a character to SL are specific to body length when growth is allometric, both proportions and dimensions must be referred to a size standard if either are to be objectively compared. For this reason, measurements and proportions used here are usually referred to a hypothetical fish of 260 mm SL, a size near the average for all specimens in the study (Table 1), and likely a common collection size. In most instances, body proportions represented by estimated dimensions at the standard size need not be limited to exactly that size for purposes of general comparison because of the proximity of allometric slopes to unity (Table 2). The data

TABLE 2.—Parameters for linear regressions (data $\log_{10}$ transformed) of measurements on standard length (mm) for Pacific ocean perch sampled from the Bering Sea (Atka-Bering region) to Vancouver Island, British Columbia. Slopes in italics are significantly different from one ($P \leq 0.05$). ANCOVA indicates significance of tests for geographic variation over the six zones by analysis of covariance (if slopes tested significantly different, intercepts were not tested).

	Males				Females			
Region	*N*	Intercept	Slope	R^2	*N*	Intercept	Slope	R^2
			NAPE					
Atka-Bering	168	−0.57942	*1.04767*	0.986	215	−0.54925	*1.03434*	0.988
Atka-Gulf	196	−0.49916	1.01264	0.946	197	−0.59329	*1.05137*	0.964
Kodiak	150	−0.52788	*1.02511*	0.984	144	−0.50253	1.01401	0.989
Yakutat	66	−0.52515	1.02721	0.965	102	−0.37849	0.96596	0.960
Southeastern	103	−0.52149	*1.02716*	0.984	65	−0.31086	*0.92727*	0.983
Vancouver	45	−0.60283	1.06479	0.957	24	−0.55937	1.04431	0.947
ANCOVA		—	***			—	***	
			SPINOUS DORSAL-FIN LENGTH					
Atka-Bering	168	−0.46575	1.00808	0.970	215	−0.51738	*1.03007*	0.984
Atka-Gulf	196	−0.48033	1.01155	0.938	197	−0.53388	*1.03434*	0.950
Kodiak	151	−0.40715	0.98179	0.968	144	−0.47812	1.01100	0.937
Yakutat	65	−0.41767	0.98430	0.945	103	−0.60298	*1.06233*	0.939
Southeastern	104	−0.65332	*1.07876*	0.965	66	−0.66303	*1.08146*	0.975
Vancouver	45	−0.18623	*0.88693*	0.887	24	−0.46602	1.00011	0.895
ANCOVA		—	***			***	NS	
			HIND-TRUNK DORSAL					
Atka-Bering	168	−0.34928	*0.96296*	0.977	213	−0.31407	*0.94808*	0.981
Atka-Gulf	196	−0.43921	1.00161	0.932	197	−0.34965	*0.96475*	0.958
Kodiak	151	−0.52480	*1.03743*	0.977	144	−0.49997	1.02683	0.973
Yakutat	65	−0.48155	1.01525	0.965	103	−0.48653	1.01744	0.955
Southeastern	104	−0.31689	*0.94900*	0.976	66	−0.55759	*1.05007*	0.978
Vancouver	45	−0.43589	0.99412	0.900	24	−0.52323	1.02901	0.930
ANCOVA		—	***			—	***	
			HIND-TRUNK VENTRAL					
Atka-Bering	168	−0.36545	*0.95394*	0.976	215	−0.17229	*0.86822*	0.970
Atka-Gulf	196	−0.36803	0.95720	0.908	197	−0.15326	*0.86477*	0.908
Kodiak	151	−0.30535	*0.93808*	0.928	144	−0.14297	*0.86656*	0.942
Yakutat	65	−0.21169	*0.89828*	0.900	103	−0.10019	*0.84914*	0.872
Southeastern	104	−0.36519	*0.96875*	0.978	66	−0.30279	*0.94197*	0.980
Vancouver	45	−0.15815	*0.88163*	0.942	24	−0.06116	*0.79192*	0.804
ANCOVA		***	NS			***	NS	
			BELLY					
Atka-Bering	168	−0.37364	*0.94635*	0.956	215	−0.70418	*1.09162*	0.965
Atka-Gulf	196	−0.33800	*0.92788*	0.808	197	−0.62569	*1.05150*	0.906
Kodiak	151	−0.60457	1.02908	0.832	144	−0.85483	*1.14125*	0.909
Yakutat	63	−0.97655	*1.17854*	0.880	97	−1.03204	*1.20777*	0.872
Southeastern	102	−0.61599	1.01693	0.903	66	−0.83303	*1.11490*	0.919
Vancouver	45	−0.81199	1.10045	0.802	24	−1.13734	*1.24044*	0.862
ANCOVA		—	***			—	*	
			PELVIC INSERTION					
Atka-Bering	168	−0.55435	*1.06386*	0.988	215	−0.46702	*1.02686*	0.988
Atka-Gulf	196	−0.51060	*1.04589*	0.958	197	−0.55050	*1.06143*	0.976
Kodiak	151	−0.43680	1.01440	0.973	144	−0.44339	1.01430	0.982
Yakutat	61	−0.40669	1.00918	0.961	97	−0.29310	0.95993	0.959
Southeastern	104	−0.40062	1.00887	0.970	66	−0.24953	*0.94551*	0.968
Vancouver	45	−0.53731	1.06759	0.944	24	−0.54122	1.06600	0.926
ANCOVA		—	*			—	***	
			HEAD					
Atka-Bering	167	−0.66929	*1.08599*	0.985	211	−0.54938	*1.03404*	0.986
Atka-Gulf	193	−0.62867	*1.06805*	0.956	95	−0.66243	*1.08088*	0.974
Kodiak	149	−0.58928	*1.04964*	0.974	141	−0.46700	0.99665	0.987
Yakutat	65	−0.56204	1.04073	0.961	103	−0.38096	0.96489	0.962
Southeastern	104	−0.52223	1.02793	0.979	65	−0.25528	*0.91393*	0.979
Vancouver	45	−0.45179	1.00443	0.935	24	−0.41197	0.98543	0.935
ANCOVA		—	*			—	***	

NS = $P > 0.05$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.005$.

TABLE 2.—*Continued.*

Region	Males				Females			
	N	Intercept	Slope	R^2	*N*	Intercept	Slope	R^2
BODY-DEPTH PELVIC								
Atka-Bering	168	−0.51033	1.00257	0.976	215	−0.54783	*1.01989*	0.980
Atka-Gulf	196	−0.53594	1.00921	0.928	197	−0.69474	*1.07506*	0.951
Kodiak	151	−0.52962	1.00452	0.967	144	−0.62554	*1.04313*	0.982
Yakutat	65	−0.61821	1.04588	0.961	103	−0.55126	1.01765	0.946
Southeastern	104	−0.71748	*1.08660*	0.978	66	−0.64909	*1.05958*	0.982
Vancouver	45	−0.79012	*1.12032*	0.951	24	−1.02734	*1.21485*	0.973
ANCOVA		—	***			—	***	
BODY-DEPTH ANAL								
Atka-Bering	168	−0.31899	*0.88824*	0.970	215	−0.23926	*0.85418*	0.959
Atka-Gulf	196	−0.35517	*0.89788*	0.903	197	−0.31260	*0.87925*	0.930
Kodiak	150	−0.48843	*0.94820*	0.949	144	−0.48666	*0.94522*	0.972
Yakutat	66	−0.44835	0.93799	0.930	103	−0.46838	*0.94474*	0.933
Southeastern	104	−0.60709	1.00067	0.958	66	−0.69547	1.03764	0.960
Vancouver	45	−0.45563	0.94021	0.848	24	−0.47752	0.94904	0.769
ANCOVA		—	***			—	***	
CAUDAL PEDUNCLE								
Atka-Bering	168	−0.89038	*0.92634*	0.970	215	−0.75477	*0.86857*	0.964
Atka-Gulf	196	−0.96731	*0.95528*	0.932	197	−0.83252	*0.89772*	0.928
Kodiak	151	−1.03039	0.97784	0.954	144	−1.04643	0.98133	0.972
Yakutat	66	−0.90622	*0.93157*	0.947	103	−0.86913	*0.91426*	0.944
Southeastern	102	−0.98737	0.96392	0.958	66	−0.99718	0.97023	0.964
Vancouver	45	−0.86566	0.91611	0.818	24	−0.88816	0.92524	0.838
ANCOVA		—	***			—	***	
ORBIT								
Atka-Bering	168	−1.12729	1.03674	0.943	215	−0.97536	0.97242	0.949
Atka-Gulf	196	−1.02260	0.99192	0.793	197	−1.05490	1.00415	0.861
Kodiak	151	−1.07754	1.00791	0.802	144	−0.83433	*0.90505*	0.786
Yakutat	65	−0.89752	0.92381	0.866	102	−0.71441	*0.84725*	0.830
Southeastern	103	−1.16845	1.03324	0.899	66	−0.83621	*0.89158*	0.903
Vancouver	45	−0.14594	*0.62383*	0.862	24	−0.22779	*0.65647*	0.667
ANCOVA		—	***			—	**	
LONGEST PECTORAL-FIN RAY								
Atka-Bering	168	−0.64359	1.02265	0.970	215	−0.53922	*0.97618*	0.978
Atka-Gulf	196	−0.63481	1.01701	0.937	197	−0.51453	*0.96360*	0.948
Kodiak	151	−0.55655	0.98090	0.947	144	−0.44668	*0.93236*	0.961
Yakutat	66	−0.72067	1.04225	0.923	102	−0.61357	0.99762	0.942
Southeastern	101	−0.88825	1.12077	0.968	66	−0.78218	*1.07402*	0.956
Vancouver	45	−0.50319	0.96330	0.901	23	−0.73958	1.05622	0.934
ANCOVA		—	**			—	**	
UPPER-JAW LENGTH								
Atka-Bering	168	−1.07654	*1.10238*	0.947	215	−0.92793	*1.03735*	0.955
Atka-Gulf	196	−1.11966	*1.12050*	0.854	195	−1.04190	*1.08558*	0.910
Kodiak	151	−0.84319	1.00090	0.898	144	−0.65487	*0.91998*	0.932
Yakutat	64	−0.64407	0.91575	0.788	101	−0.57472	*0.88516*	0.770
Southeastern	104	−0.99592	1.06287	0.838	66	−0.81778	0.98171	0.819
Vancouver	45	−0.52744	0.86802	0.711	24	−0.16892	*0.72101*	0.651
ANCOVA		—	***			—	***	
UPPER-JAW WIDTH								
Atka-Bering	168	−1.37815	1.03050	0.891	215	−1.38585	1.02967	0.915
Atka-Gulf	196	−1.49225	1.07165	0.804	197	−1.41203	1.03808	0.838
Kodiak	151	−1.23784	0.96166	0.776	143	−1.20719	0.94924	0.880
Yakutat	66	−1.31512	1.00107	0.844	103	−1.20986	0.95659	0.839
Southeastern	104	−1.56596	*1.11473*	0.880	66	−1.00614	*0.87986*	0.881
Vancouver	45	−1.91421	*1.25943*	0.775	23	−1.81392	1.21350	0.748
ANCOVA		—	*			—	***	

NS = $P > 0.05$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.005$.

TABLE 2.—*Continued.*

Region	Males N	Males Intercept	Males Slope	Males R^2	Females N	Females Intercept	Females Slope	Females R^2
SYMPHYSEAL KNOB								
Atka-Bering	166	−3.09541	*1.56992*	0.769	215	−2.81549	*1.44987*	0.814
Atka-Gulf	196	−2.80011	*1.43432*	0.540	197	−2.87970	*1.46848*	0.576
Kodiak	151	−3.82404	*1.87456*	0.876	144	−3.23909	*1.63193*	0.857
Yakutat	66	−3.01114	*1.52401*	0.785	103	−2.54090	*1.32784*	0.714
Southeastern	104	−2.53152	*1.32159*	0.808	65	−3.23953	*1.60663*	0.817
Vancouver	45	−2.90945	*1.47650*	0.638	24	−2.42106	1.28184	0.570
ANCOVA		—	***			***	NS	
6TH SPINOUS RAY IN DORSAL FIN								
Atka-Bering	167	−0.94686	1.00886	0.882	209	−0.79653	*0.94481*	0.900
Atka-Gulf	194	−0.99815	1.03241	0.735	191	−1.07166	1.05966	0.783
Kodiak	148	−0.82023	0.95342	0.836	136	−0.62671	*0.86982*	0.845
Yakutat	64	−1.19498	1.10184	0.818	97	−0.91257	0.98441	0.800
Southeastern	90	−1.17989	*1.10021*	0.894	59	−1.00276	1.02520	0.877
Vancouver	44	−0.64705	0.88566	0.616	19	−0.81268	0.94818	0.649
ANCOVA		***	NS			—	**	
13TH SPINOUS RAY IN DORSAL FIN								
Atka-Bering	165	−0.87157	*0.91366*	0.804	208	−0.72181	*0.85087*	0.834
Atka-Gulf	192	−0.98173	0.96415	0.621	183	−1.02884	0.98308	0.730
Kodiak	141	−0.85834	*0.91216*	0.766	133	−0.90253	0.92803	0.780
Yakutat	63	−0.94187	0.94260	0.771	87	−0.85833	0.90897	0.744
Southeastern	95	−0.79462	*0.88878*	0.816	57	−0.95486	0.95753	0.783
Vancouver	42	−0.39052	0.73692	0.394	20	−1.10477	1.01967	0.638
ANCOVA		***	NS			***	NS	
3D ANAL-FIN SPINE								
Atka-Bering	147	−0.50863	*0.81717*	0.849	190	−0.39317	*0.76948*	0.865
Atka-Gulf	166	−0.24648	*0.71104*	0.682	172	−0.18951	*0.68697*	0.696
Kodiak	131	−0.36994	*0.75870*	0.785	126	−0.32305	*0.73849*	0.818
Yakutat	62	−0.14422	*0.66714*	0.690	93	−0.45754	*0.79909*	0.714
Southeastern	66	−0.15004	*0.67029*	0.061	44	−0.54744	*0.82184*	0.742
Vancouver	40	+0.33516	*0.46515*	0.374	19	+0.28173	*0.48651*	0.451
ANCOVA		—	***			***	NS	

NS = $P > 0.05$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.005$.

agree with visual impressions of negligible proportional changes with growth, gained from working with the species in the field.

To compare measurement variability for sexual and geographic factors in untransformed data, in the section on character discrimination, I obtained symmetrical estimates of variation about mean values by taking limits formed by one standard deviation (about each regression by sex within region) on each side of the transformed means. I then back-transformed the limits and halved the difference between them. This symmetrical substitute for the asymetrical standard deviation about regression is called the "alternate standard deviation".

Westrheim (1975) studied sexual maturity in Pacific ocean perch from the Gulf of Alaska and concluded that onset occurred between 195 and 260 mm SL [fork length (FL) converted to SL by relationships established from the present morphometric data: SL=−3.272+0.879 FL, where N=1,528 and R^2=0.997]. In the present study, the boundary between juveniles and adults is taken as 230 mm SL.

Body Form Varied Geographically and by Sex

Although later, more detailed, analyses disclosed that the constant slopes required by the ANCOVA program BMDP P2V (Dixon et al. 1977) for each character (transformed data) were technically unmet, a preliminary analysis with this program indicated likely significant geographic and sexual variation in all characters (subsequently confirmed in detailed analyses with a more general ANCOVA model, Table 2), and a general lack of interaction between these factors. Also, I determined that only negligible bias has been induced in the regressions by logarithmic transformation of data by computing mean response variables, at 260 mm SL, for untransformed measurements fit by nonlinear least squares (BMDP PAR, Dixon et al. 1977). For six

measurements, by sex and region, over which the two methods were compared, the prediction of character sizes in fish of 260 mm SL by nonlinear least squares was close to the mean and within the 95% confidence interval for prediction from transformed data (Fig. 2) and did not change the results.

Graphical comparison of character measurements, related to the standardized fish of 260 mm SL, also disclosed that geographic and sexual variation were frequent:

Nape (Fig. 2A).—Geographic variation in distance between tip of snout and the dorsal fin was significant. Napes averaged shortest in the Atka-Gulf and Kodiak regions and lengthened in a cline to the Vancouver region. Females averaged smaller napes than males in all regions.

Spinous dorsal-fin length (Fig. 2B).—Geographic variation in length of spinous dorsal fin was significant, and the fin shortened in a cline from the Bering Sea to the Southeastern and Vancouver regions. Because geographic variation in length of the spinous dorsal fin was nearly opposite to geographic variation in the nape, changes in position of the anterior fin insertion probably caused the reciprocal clines. Sexual dimorphism was not important.

Hind-trunk dorsal (Fig. 2C).—Distance between the spinous dorsal fin and the tail changed significantly between regions. It averaged largest in specimens from the middle regions (Atka-Gulf and Kodiak) and smallest in the Vancouver region. Sexual dimorphism was not important.

Hind-trunk ventral (Fig. 2D).—Distance between the second spine of the anal fin and the tail changed significantly between regions. It averaged largest in the Southeastern and Vancouver regions and shortest in the Atka-Bering region. The data formed a geographic cline opposite to that of the belly measurement. From the Yakutat region westward, females averaged significantly shorter in this measurement than males.

Belly (Fig. 2E).—Distance between the pelvic fins and anal-fin spines varied significantly geographically and decreased in a cline from northwest to southeast (Atka-Bering region to the Southeastern and Vancouver regions). Belly measurements averaged about 1.6 cm smaller in the southeastern extreme of the sampling range than in the northwestern. The cline apparently is caused by opposing relational movements of pelvic girdle and anal-fin spines along the body axis because the pelvic insertion and hind-trunk ventral measurements decreased from southeast to northwest. Sexual dimorphism was significant, with bellies of males averaging about 4 mm smaller than those of females.

Pelvic insertion (Fig. 2F).—Geographic variation in distance between snout and pelvic fins was significant, and the distance increased from northwest to southeast, from the Atka-Bering region to the Vancouver region. The measurement averaged shorter in females than males in all regions, evidence for significant sexual dimorphism.

Head (Fig. 2G).—Geographic variation in head length was significant, and heads averaged shortest in the Kodiak region and longest in the Vancouver region. Sexual dimorphism was usually significant, and females averaged smaller heads than males. Trends in geographic and sexual variation between the head and pelvic insertion were similar, probably because both measurements include similar regions of the head.

Body-depth pelvic (Fig. 2H).—Geographic variation in body depth at the pelvic fins was significant and formed a broken cline. Deepest bodies occurred at the extremes of the sampling range (Atka-Bering and Vancouver regions), and were shallowest in the Kodiak region. Sexual dimorphism was inconsistent.

Body-depth anal (Fig. 2I).—Geographic variation in body depth at the anal spines was significant, and depth was shallowest in Kodiak specimens and deepest in Atka-Bering specimens. Body depths averaged smaller in females than in males from the Yakutat region to the Atka-Bering region, but the differences may not be significant.

Caudal peduncle (Fig. 2J).—Geographic variation in depth of caudal peduncle was significant, but important geographic differences were limited to regions west of Yakutat. Specimens from the Kodiak region averaged narrowest peduncles, and specimens from the Atka-Bering, Southeastern, and Vancouver regions averaged widest peduncles. Caudal peduncles averaged significantly narrower in females than in males except in the Southeastern and Vancouver regions.

Orbit (Fig. 2K).—Geographic variation in orbit diameter was significant. Diameters were

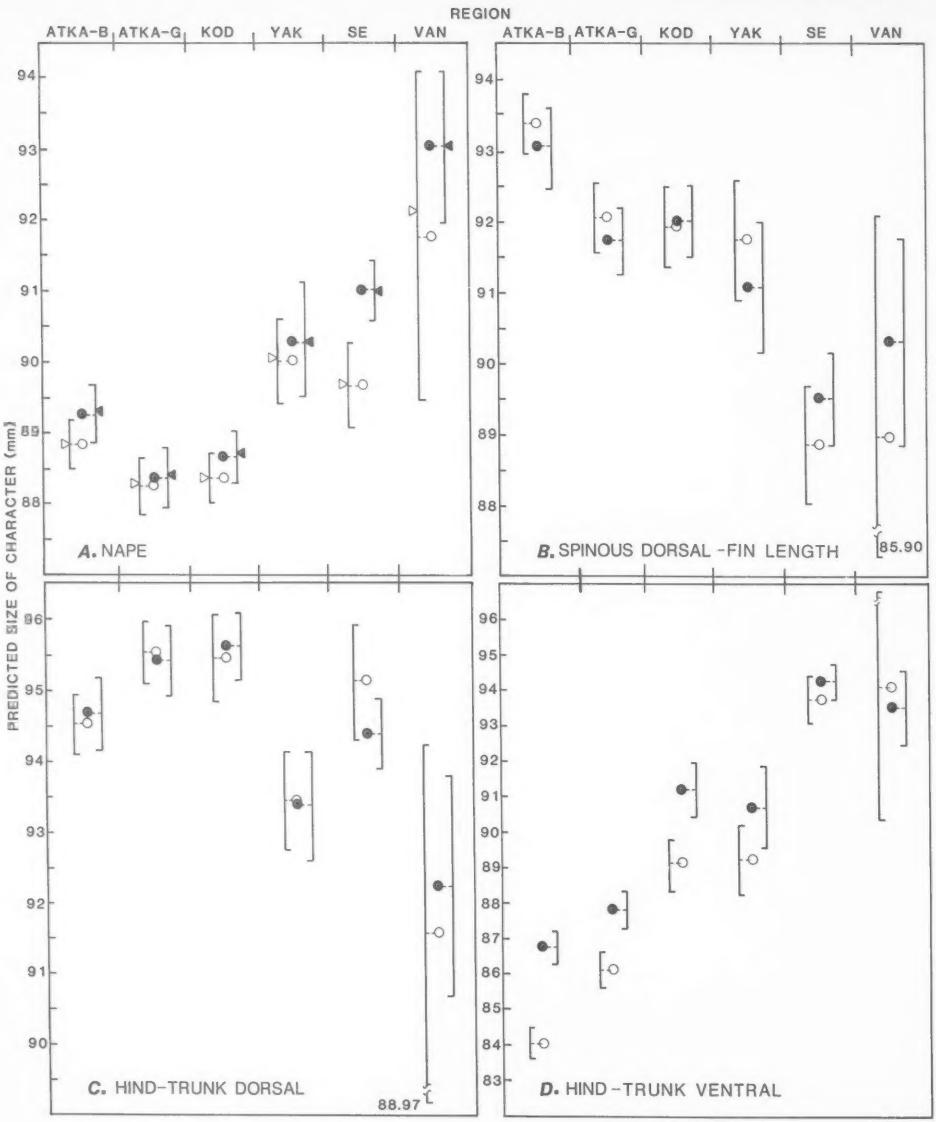

FIGURE 2.—Geographic and sexual variation in measurements of Pacific ocean perch in the northeastern Pacific Ocean and eastern Bering Sea as represented by mean responses to regression functions (Table 2) (circles) and 95% confidence intervals (brackets) for these responses as related to a standard-sized fish of 260 mm SL. Solid symbols represent males and open symbols females. Triangles represent mean responses by nonlinear least squares analysis (Dixon et al. 1977) for 260 mm SL fish.

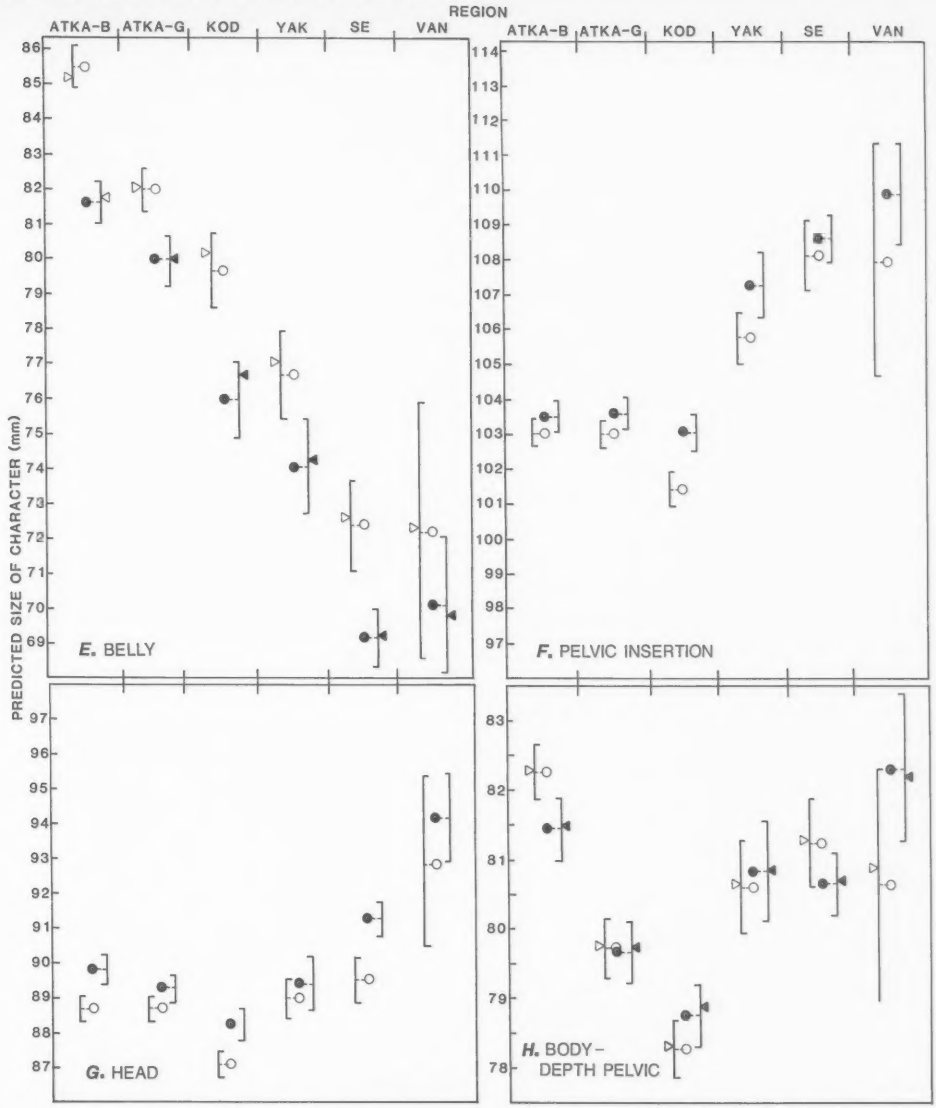

FIGURE 2.—*Continued.*

largest in the Atka-Bering and Atka-Gulf regions and smallest in the Southeastern region. Diameters decreased continuously from the Atka-Bering region to the Southeastern region, but the trend was broken by Vancouver samples. Although not significant within regions, sexual differences in orbit diameter probably were significant overall because females averaged smaller orbits than males in all regions.

Longest pectoral-fin ray (Fig. 2L).—Geographic variation in length of pectoral fins was significant. The fins averaged longest at the eastern

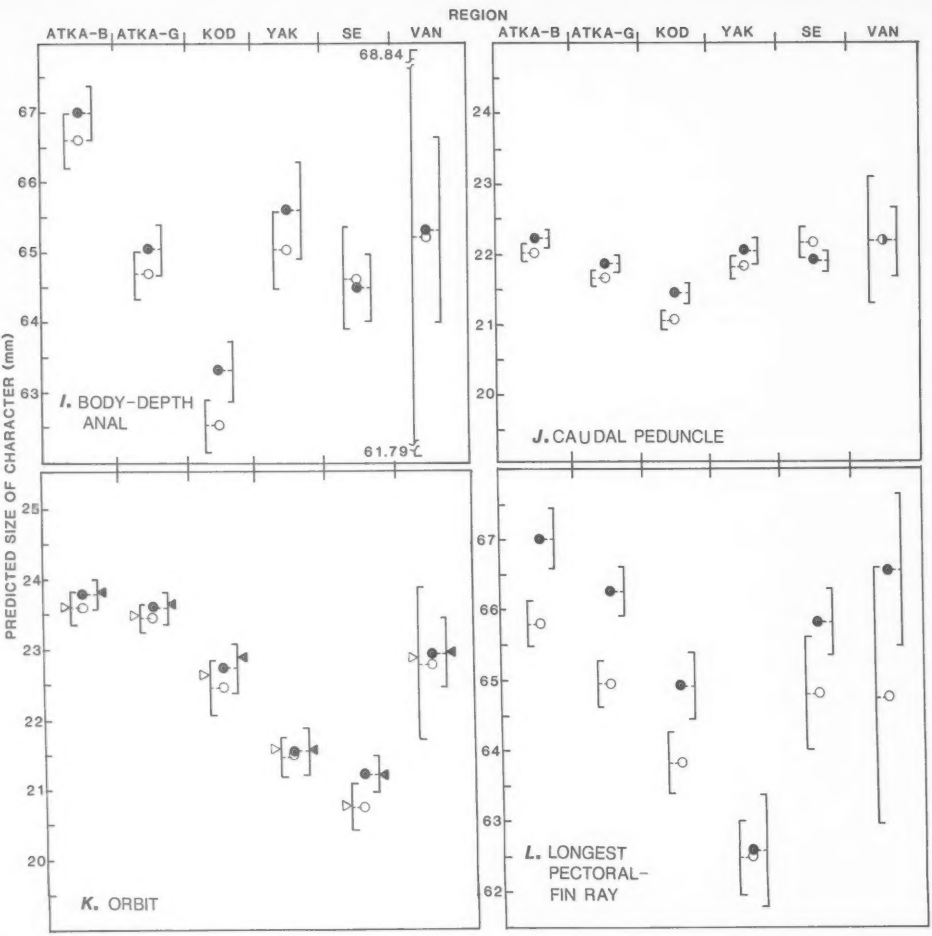

FIGURE 2.—*Continued.*

and western extremes of the sampling range and shortest in the Yakutat region. In all regions but Yakutat, sexual dimorphism was high and significant, and fins in females averaged >1 mm shorter than in males.

Upper-jaw length (Fig. 2M).—Geographic variation was significant, and jaws averaged longest in eastern Aleutian samples (Atka-Bering and Atka-Gulf regions). Sexual dimorphism was significant in three regions (Atka-Bering, Atka-Gulf, and Southeastern), with females averaging shorter upper jaws than males in each.

Upper-jaw width (Fig. 2N).—Geographic variation was significant, with upper jaws averaging narrowest in the Kodiak region. Sexual dimorphism was important in only the Atka-Bering and Southeastern regions, where females averaged narrower upper jaws than males.

Symphyseal knob (Fig. 2O).—Geographic variation was significant but erratic. On average, specimens from the Atka-Gulf region probably have the largest symphyseal knobs. Sexual dimorphism seems unimportant.

6th spinous ray in dorsal fin (Fig. 2P).—Geo-

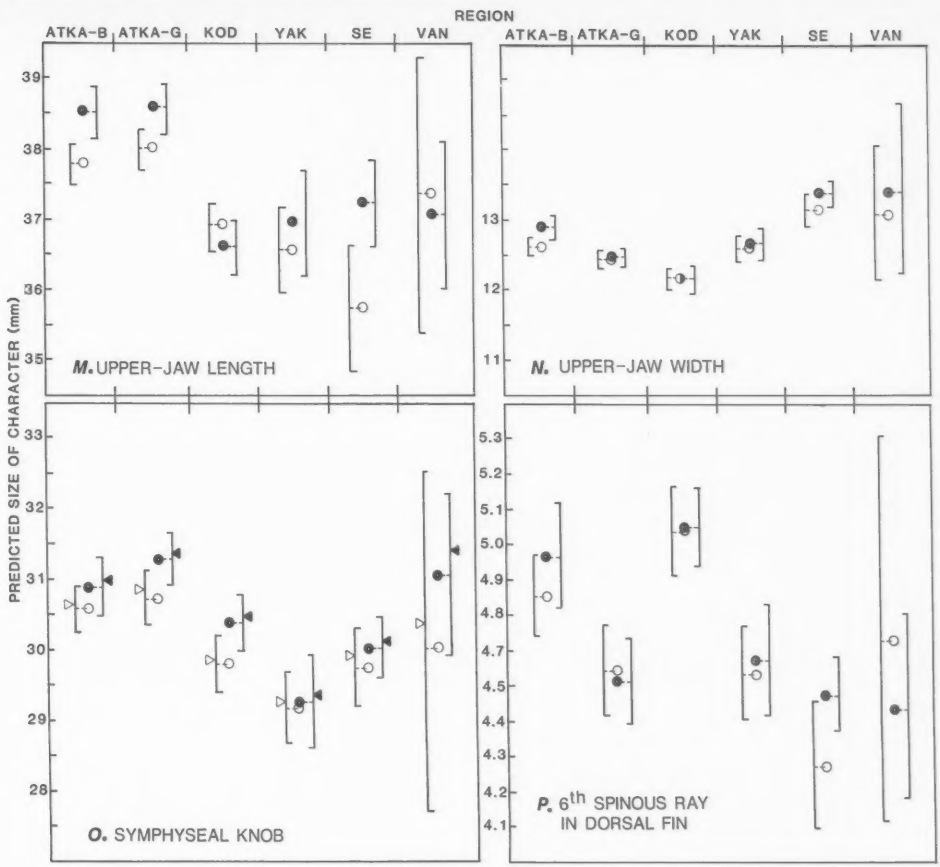

FIGURE 2.—*Continued.*

graphic variation was significant but erratic in this index to height of the spinous dorsal fin. Kodiak specimens had the highest spinous dorsal fins, on average. Sexual variation was inconsistent and is probably unimportant.

13th spinous ray in dorsal fin (Fig. 2Q).—Geographic variation was significant but erratic in this index to height of the notch between spinous and soft dorsal fins. Sexual dimorphism seems generally unimportant.

3d anal-fin spine (Fig. 2R).—Geographic and sexual variation in length of the spinous ray was minor, except that the fin spine was unusually short in females from the Southeastern region.

The measurements (as related to the standardized fish of 260 mm SL) usually varied geographically either in generally monotonic clines over the study area (Atka-Bering to Vancouver regions) or V-shaped clines that were broken in the Yakutat or Kodiak region. Only two sets of characters varied almost monotonically, and variation within each can be ascribed to a progressive shift in boundary features for body regions: Length of nape generally decreased and length of the spinous-dorsal fin increased from southeast to northwest (Fig. 2A, B), probably because of a relational shift in the dorsal-fin insertion. Belly size increased from southeast to northwest (Fig. 2E), probably because the pectoral girdle and associ-

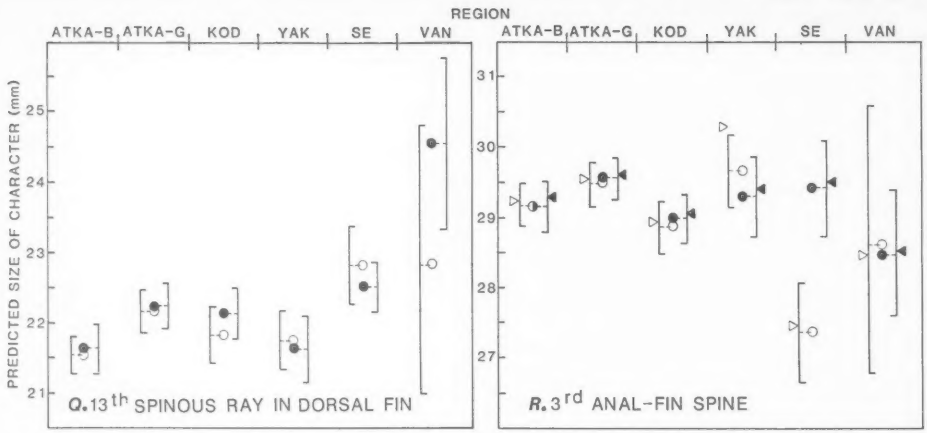

FIGURE 2.—*Continued.*

ated pelvic fins and the complex of anal-fin spines moved relationally apart (Fig. 2F, D). In contrast, depth of the entire body of Pacific ocean perch varied similarly geographically because the three measures of body depth—body-depth pelvic, body-depth anal, and caudal peduncle—varied concordantly (Fig. 3).

Sexual dimorphism was significant in most measurements, and except for belly size, measurements usually averaged larger in males than in females. The combined effects of geographic and sexual variation meant that belly measurements averaged about 16 mm larger in standard-sized females from the Atka-Bering region than in males from the Southeastern or Vancouver region (Fig. 2E).

Slopes in over one-half of the measurement regressions differed significantly from unity (Table 2), indicating growth allometry, particularly when differences from unity were consistent. The symphyseal knob was the only character with strong positive allometry (Table 2). Only two characters were strongly or consistently negatively allometric (Table 2): hind-trunk ventral, significant in 11 of 12 sex/region cells (slopes averaging 0.94 in males and 0.87 in females); and length of 3d anal-fin spine, significant in all 12 sex/region cells (slopes averaging 0.72 in males and 0.74 in females). With growth, the trunk posterior to the anal-fin spines becomes proportionally smaller relative to the rest of the body because of negative allometry in the body-depth anal, hind-trunk ventral, and caudal peduncle measurements.

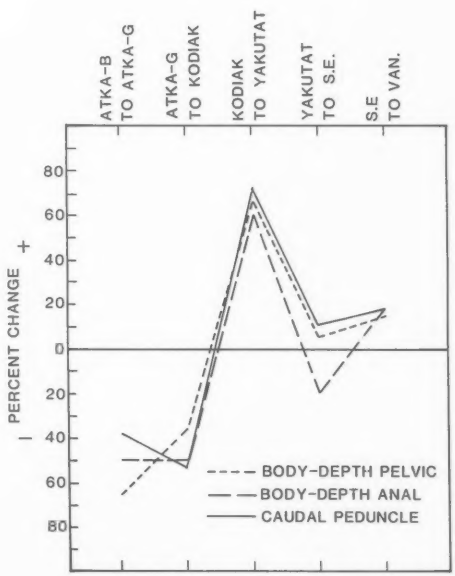

FIGURE 3.—Geographic variation in depth measurements of three body characters in Pacific ocean perch. Character measurements were related to a standard-sized fish of 260 mm SL from regressions in Table 2, then back transformed. Because measurements for males and females were usually different (Fig. 2), midvalues between sexes were used. Percentage change is the change in a measurement between neighboring regions as a percentage of the measurement's range over the geographic range.

Inflections and Sexual Crossover in the Regressions

I examined 216 computer-drawn scattergrams for sexes within regions that represented the measurement regressions (Table 2), by transparent overlay with incised straight line. None shows obvious curvature, and only three show possible inflections: In females, the regression appears to bend upward about 8.3° at about 262 mm SL for belly measurements in the Atka-Bering region; downward about 7.0° at about 242 mm SL for hind-trunk ventral in the same region; and possibly upward about 13.5° at about 260 mm SL for the belly in the Southeastern region. Whether the apparent breaks in the three regressions are artifacts or real is moot. Evidence for reality includes their visibility in scattergrams; that all occur in a single sex (females) and in a measurement possibly influenced by sexual development with growth; and that the possible break in the belly regression in the Atka-Bering region has a near complement in the hind-trunk ventral measurements, which extend from the belly to the tail. Also, as discussed in a succeeding paragraph, mild inflections probably are hidden in variability of the data. Evidence against reality includes the extreme rarity of visible indications of possible breaks (none in 16 of 18 measurements and only 3 in the remaining 24 regressions), and the extreme goodness of fit (R^2) to a straight line shown by the regressions with possible inflections (Table 2). The measures for goodness of fit for belly are the best among regions in the two regressions with possible inflections, and both measures are higher than those for corresponding male regressions, which show no indications of inflection. The weight of evidence seems to side with the visible breaks being artifacts. Yet, even if the breaks represent real inflections, the morphometric data seem to fit linear criteria well as far as conventional measures are concerned.

The regressions for sexes, within measurements and regions (Table 2), diverge with increasing SL, indicating that sexual dimorphism increases with growth. The increases are slight, however, as evidenced by the similarity in regression parameters between sexes, and on average, characters will differ in size between sexes by only a few millimeters in the standard 260 mm SL fish (Fig. 2). Given normal variation, the differences should not be obvious or reliable in differentiating sexes by gross examination of even the largest Pacific ocean perch.

However, divergent sexual-regression pairs pose an apparent contradiction when they intersect within their data domain. Such intersections infer 1) sexual differences in fish on the juvenile side of the intersection, 2) differences on the juvenile side the reverse of those on the adult side, and 3) differences between sexes in juveniles that increase as SL's become smaller. In the morphometric data, the regressions for sexes do intersect, and the intersections form a symmetrical unimodal distribution with a strong peak near 230 mm SL. By itself, crossover need not be a problem; e.g., the symmetrical confidence limits about regression (Sokal and Rohlf 1969) are evidence that crossover within these limits is normal in samples from a single population. Yet, differences in measurements for sexes on the juvenile side of the modal point for sexual crossovers apparently are greater than can be accommodated by confidence limits based on the regressions. In 108 comparisons of mean estimates for measurements and their confidence limits at 170 mm SL, 18 have significant differences, when only about 5 are expected with 95% confidence limits. Apparently, sexually associated crossover is slightly too severe in the morphometric data to be adequately contained by confidence limits for single populations.

The evidence is strong that most of the measurement regressions do not fit their data perfectly and, because of the nature of the error, that slight growth inflections likely are concealed by variation. The three apparent inflections mentioned previously might indicate the size at inflection, but the evidence is weak. It is apparent, however, that significant sexual differences in measurements at SL's below the crossover mode should not be taken literally. (Assuming that measurement regressions may incorporate hidden inflections, most reliable estimates of juvenile measurements among sexual pairs within their data domains will be from the regression whose slope is nearest unity, particularly if the sample number is large and the slope not significantly different from unity.) Because the bulk of specimens were larger than 230 mm SL, and the regressions fit their data closely, conclusions regarding adult relationships in the present data, particularly trends, should be reliable.

Strength of Geographic and Sexual Variation Shown in the Characters

Analysis of morphological diversity is most use-

ful where assigned components of variation can be maximized relative to unassigned components. I compared indices of variation assignable to measurement size (standard specimens), geographic, and sexual causes in the 18 characters by means of the alternate standard deviation (see Methods). First, I investigated relationships between variation and the size of a character. When mean responses for measurements in standard-sized fish from the Kodiak region were used as a basis of comparison, variability was positively related to size of the character, with the two variates significantly correlated (Fig. 4).

Size accounted for about 62% (R^2) of the variation between characters. To remove its effect in further comparisons, I used an alternate version of the coefficient of variation; i.e., the alternate standard deviation for each character divided by a size index (Kodiak) for that character $\times 100$. Although the alternate coefficient of variation reduced the unassigned variability, some sizable differences remained between characters (Table 3)—major dimensions of the head and dorsum varied least, fin spines and small features of the head varied most, and the symphyseal knob varied considerably more than any other character. With the exception of belly, the major trunk

TABLE 3.—Evidence for unassigned variation in measurements in Pacific ocean perch after correction for measurement size. Measurements ($\hat{Y}$) are related to a standard-sized fish of 260 mm SL from the Kodiak region by regressions in Table 2. Relative variation for each measurement is indexed by the alternate coefficient of variation (ACV) (see text) pooled over all regions and expressed as a percentage. Measurements arranged by increasing alternate coefficient of variation in the last column.

	Males		Females		Both sexes	
Measurement	$\hat{Y}$, mm	ACV	$\hat{Y}$, mm	ACV	$\hat{Y}$, mm	ACV
Nape	88.66	2.50	88.36	2.29	88.52	2.40
Head	88.22	3.32	87.07	2.53	87.66	2.94
Pelvic insertion	103.03	3.20	101.42	3.01	102.24	3.11
Body-depth pelvic	78.75	3.53	78.27	3.04	78.52	3.29
Hind-trunk dorsal	95.62	3.01	95.46	3.72	95.54	3.36
Spinous dorsal-fin length	92.01	3.43	91.92	3.63	91.97	3.53
Body-depth anal	63.31	4.19	62.52	3.51	62.92	3.86
Caudal peduncle	21.43	4.08	21.06	3.65	21.25	3.87
Longest pectoral-fin ray	64.91	4.43	63.82	4.10	64.38	4.27
Hind-trunk ventral	91.22	4.98	89.07	4.69	90.07	4.84
Upper-jaw length	36.60	6.43	36.89	5.43	36.74	5.94
3d anal-fin spine	28.99	6.68	28.87	6.61	28.93	6.64
6th spinous ray in dorsal fin	30.36	7.92	29.78	7.58	30.08	7.76
Belly	75.97	8.82	79.66	7.87	77.77	8.36
Upper-jaw width	12.15	9.86	12.17	7.54	12.16	8.73
13th spinous ray in dorsal fin	22.11	9.45	21.81	10.05	21.96	9.74
Orbit	22.73	9.57	22.46	10.32	22.60	9.94
Symphyseal knob	5.05	13.51	5.04	14.59	5.04	14.04

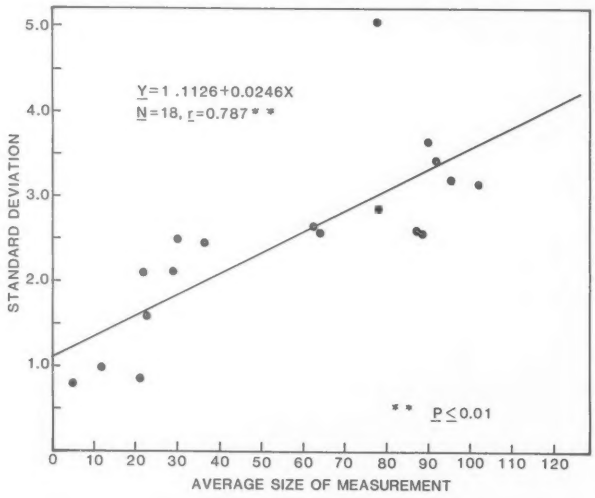

FIGURE 4.—Relationship between absolute size and variability of measurements in Pacific ocean perch. Character sizes are mean responses for hypothetical 260 mm SL fish from the Kodiak region as estimated from the regressions of Table 2; variability is estimated by alternate standard deviations for each character (see Methods) pooled over all regions.

dimensions had the lowest unassigned variability when corrected for size.

As would be expected from the plots of character measurements (Fig. 2), sexual and geographic variation were important components after the size effects were removed (Table 4). For sexual variation, the hind-trunk dorsal, spinous-dorsal fin, and body-depth pelvic measurements were the poorest discriminators, and belly, hind-trunk ventral, and longest pectoral-fin ray the best. For geographic variation, 3d anal-fin spine, symphyseal knob, and 6th spinous ray in dorsal fin were the poorest discriminators, and belly, hind-trunk ventral, and head measurements the best.

Present Nominal Subspecies are Questionable

Barsukov (1964) synonymized the nominal species *Sebastodes alutus* (Gilbert) and *S. paucispinosus* (Matsubara) but suggested that the eastern and western Pacific representatives may be separate subspecies: *S. a. paucispinosus* ranging from Honshu to Olyutorskii Bay and along the northern Bering Sea slope, perhaps to Bristol Bay; and *S. a. alutus* ranging from California to the Gulf of Alaska and along the Aleutian Arc to, and including, the Commander Islands. Barsukov morphologically distinguished the subspecies by "Alaskan *Seb. alutus* longer than 23 cm are quite noticeably distinguished from *Seb. alutus* from other parts of the range by body depth", and in a key gives the principal subspecies discriminator as whether the ratio SL/body depth of 170-360 mm SL fish is greater than 3.2 (*S. a. alutus*) or less (*S. a. paucispinosus*).

The question of eastern and western subspecies in *S. alutus* seems more complex than Barsukov (1964) suggested. The weight of present evidence, although preliminary, does not seem to justify the nominal subspecies. First, there is the problem of how populations sympatric over a distance as great as the Aleutian Arc could maintain reproductive isolation adequate to insure genetic distinctiveness. There is no evidence for isolating mechanisms in the species—on the contrary, the larvae are pelagic (Hart 1973), which should promote rapid genetic exchange over major distances

TABLE 4.—Relative degree that measurements in standard-sized Pacific ocean perch of 260 mm SL reveal geographic and sexual variation. In the variation sections, variation not related to character size was indexed by alternate coefficients of variation that were pooled over all samples, sexual variation was indexed by differences between sexes as a percentage of their mid-size in each region (positive if males averaged larger than females and negative if males were smaller, but only absolute values were used in calculations), and geographic variation was indexed by the maximum difference between regions as a percentage of mean-estimate size of measurements from the Kodiak region (Table 3). In the discrimination section, indices indicate relative magnitudes of sexual and geographic variation relative to variation not related to character size. Low values or ranks (in parentheses) indicate that variation not related to character size was high relative to sexual (data column 4) or geographic (data column 5) variation; hence, the measurement is a poor indicator of sexual or geographic variation, and vice versa. Kendall Coefficient of Concordance (Siegel 1956) between ranks for sexual and geographic variation was not significant.

Character	Variation not related to character size	Relative variation		Discrimination	
		Sexual	Geographic	(Sexual ÷ col. 1) × 10	Geographic ÷ column 1
Nape	2.91 (1)	0.493 (4)	4.60 (7)	1.69 (10)	1.58 (13)
Spinous dorsal-fin length	3.73 (6)	(−)0.088 (2)	4.39 (5)	0.24 (2)	1.18 (9)
Hind-trunk dorsal	3.35 (4)	(−)0.019 (1)	3.80 (2)	0.06 (1)	1.13 (7.5)
Hind-trunk ventral	4.05 (9)	2.038 (17)	9.57 (15)	5.03 (17)	2.36 (17)
Belly	6.45 (11)	(−)3.873 (18)	16.47 (18)	6.00 (18)	2.55 (18)
Pelvic insertion	3.08 (3)	0.875 (11)	6.53 (12)	2.84 (14)	2.12 (15)
Head	3.07 (2)	1.104 (13)	6.69 (13)	3.60 (15)	2.18 (16)
Body-depth pelvic	3.63 (5)	(−)0.104 (3)	4.32 (4)	0.29 (3)	1.19 (10)
Body-depth anal	4.21 (10)	0.628 (8)	6.19 (11)	1.49 (9)	1.47 (11)
Caudal peduncle	4.02 (7.5)	0.828 (9)	4.53 (6)	2.06 (13)	1.13 (7.5)
Orbit	7.01 (13)	0.503 (5)	13.39 (17)	0.72 (6)	1.91 (14)
Longest pectoral-fin ray	4.02 (7.5)	1.663 (16)	6.03 (10)	4.14 (16)	1.50 (12)
Upper-jaw length	6.68 (12)	1.305 (14)	4.93 (8)	1.95 (12)	0.74 (4)
Upper-jaw width	8.09 (15)	0.970 (12)	9.03 (14)	1.20 (8)	1.12 (6)
Symphyseal knob	15.49 (18)	0.873 (10)	11.29 (16)	0.56 (4)	0.73 (2.5)
6th spinous ray in dorsal fin	8.21 (16)	1.410 (15)	5.97 (9)	1.72 (11)	0.73 (2.5)
13th spinous ray in dorsal fin	9.54 (17)	0.589 (6)	0.94 (1)	0.62 (5)	0.99 (5)
3d anal-fin spine	7.31 (14)	0.602 (7)	3.87 (3)	0.82 (7)	0.53 (1)

and erase local differentiation. Further, the species appears to be genetically nearly homogeneous over as great, and environmentally variable, a distance in the eastern part of its range—Seeb and Gunderson (in press) demonstrated "very high similarity" among populations from Washington State to the Bering Sea and found no evidence for a barrier at the Aleutian Chain. Second, as already mentioned, morphological (including morphometric) differences can be environmentally induced through modification of growth rate. The growth differences Quast (fn. 2) found, which appeared to conform more closely to latitude than ocean temperatures, resemble geographic trends in some measurements examined in the present study, including body-depth pelvic (Fig. 2H). Last, Barsukov's criteria for the subspecies can be called into question. When referred to fish of two standard sizes, 260 and 300 mm SL, my data on body-depth pelvic (Barsukov's "body depth") indicate that only representatives from the Kodiak region have 95% confidence limits for *mean* population values that lie consistently on the *S. a. alutus* (the nominal eastern subspecies) side of Barsukov's criterion–confidence limits for most measurement means for other regions indicate ambiguous or improper identification (Table 5), and that a majority of specimens will be improperly identified. Further, neighboring populations in the eastern subspecies' range frequently differ significantly in one or more measurements (Fig. 2, Table 2). If significant geographic variation were a sole criterion for subspecies then a number might need be named.

Barsukov (1964) gave further criteria for separating the nominal eastern and western subspecies, but the criteria seem subjective and impractical: Prominence and apparent squamation of occipital crests do not seem of value; as I have observed, development of crests may be highly variable within regions, and evidence for squamation can be altered in specimens collected by bottom trawl. His analysis of variation in the occipital crests is too short and subjective to be useful. Size of symphyseal knob ("larger at similar body lengths in the eastern subspecies") is not reliable because the character has considerable

TABLE 5.—Mean, upper, and lower 95% confidence limits for the mean of body-depth pelvic (BDP) measurements and their derived proportions of standard length (SL) for Pacific ocean perch of 260 and 300 mm SL. Ratios of SL divided by body depth are categorized according to Barsukov's (1964) criterion of 3.2 for the ratio as follows: Ratios rounding to greater than the interval 3.15-3.24 (3.2 expanded to its inclusive values with two decimal points) are followed by a blank, those within the interval are followed by an "A", and those lower are followed by an "I". Ratios followed by a blank would identify the eastern nominal subspecies (*S. a. alutus*) by the 3.2 criterion, those followed by an "A" would give an ambiguous identification (*S. a. alutus* or *S. a. paucispinosus*), and those followed by an "I" would identify the western nominal subspecies (*S. a. paucispinosus*).

Region (limit)	260 mm SL				300 mm SL			
	Males		Females		Males		Females	
	BDP	SL/BDP	BDP	SL/BDP	BDP	SL/BDP	BDP	SL/BDP
Atka-Bering								
Lower	81.909	3.17 A	82.665	3.15 A	94.715	3.17 A	95.717	3.13 I
Mean	81.422	3.19 A	82.258	3.16 A	94.006	3.19 A	95.183	3.15 A
Upper	80.957	3.21 A	81.853	3.18 A	93.302	3.22 A	94.652	3.17 A
Atka-Gulf								
Lower	80.115	3.25	80.145	3.24 A	92.859	3.23 A	93.687	3.20 A
Mean	79.666	3.26	79.708	3.26	92.044	3.26	92.964	3.23 A
Upper	79.219	3.28	79.274	3.28	91.236	3.29	92.247	3.25
Kodiak								
Lower	79.214	3.28	78.662	3.31	91.513	3.28	91.554	3.28
Mean	78.753	3.30	78.269	3.32	90.928	3.30	90.870	3.30
Upper	78.295	3.32	77.878	3.34	90.346	3.32	90.389	3.32
Yakutat								
Lower	81.560	3.19 A	81.271	3.20 A	94.997	3.16 A	94.278	3.18 A
Mean	80.828	3.22 A	80.600	3.23 A	93.877	3.20 A	93.236	3.22 A
Upper	80.102	3.25	79.934	3.25	92.770	3.23 A	92.186	3.25
Southeastern								
Lower	81.125	3.20 A	81.878	3.18 A	94.906	3.16 A	95.531	3.14 I
Mean	80.655	3.22 A	81.239	3.20 A	94.224	3.18 A	94.540	3.17 A
Upper	80.187	3.24 A	80.605	3.23 A	93.547	3.21 A	93.559	3.21 A
Vancouver								
Lower	83.391	3.12 I	82.356	3.16 A	97.376	3.08 I	97.027	3.09 I
Mean	82.304	3.16 A	80.629	3.22 A	96.616	3.11 I	95.938	3.13 I
Upper	81.231	3.20 A	78.958	3.29	95.861	3.13 I	94.861	3.16 A

unassigned variation for its size (Table 3), as well as high positive allometry (Table 2).

The possibility exists, since Barsukov (1964) measured body depth directly on preserved specimens, a method different from that used in the present paper, that the two methods give biased measurements relative to the other. The question cannot be fully resolved; Barsukov gave sparse collection information (e.g., his conclusions on Bristol Bay representatives were based on eight or fewer specimens between 30 and 340 mm SL), and he gave no data on statistical parameters or data peculiarities. Although the body depth measurement at pelvic fins is simple to perform, high accuracy and undistorted material are necessary because geographic variation is slight but significant (e.g., maximum geographic difference between means for body-depth pelvic at 260 mm SL is around 4 mm in Figure 2H).

Indirect evidence indicates that the combination of photogrammetry and fresh specimens used in the present study probably gave more precise measurements than the hand methods and museum specimens used by Barsukov (1964), but likely that bias between methods was unimportant relative to other factors. Barsukov stated that body depth in specimens attributed by him to *S. a. paucispinosus*, presumably including those from Bristol Bay, averages 3.05 into SL, and that his specimens of *S. a. alutus* average 3.42. In contrast, in the present study, the extreme regional confidence limits for means lie between 3.08 and 3.34 (Table 5), well within the span of Barsukov's means (my data for Bristol Bay are nearly central between his values, with confidence limits of 3.12 and 3.22).

Rather than methods bias, the wide range of mean values for body depth given by Barsukov (1964) relative to those in Table 5 may have been caused in part by chance overweighting of extreme data values because of his relatively small sample sizes. His 124 specimens were relatively few for a considerable geographic range—82 from Bristol Bay to Washington and 42 from Olyutorskii Bay and the Commander Islands. Perhaps, body-depth variation was falsely indicated as bimodal in Aleutian Arc representatives, leading to the interpretation that the data represented shallow- and deep-bodied populations.

Finally, Barsukov may have been misled by variable distortion and shrinkage of his specimens owing to conditions of preservation and storage. Although he stated that his specimens shortened 0.3-4.0% after "several" months of preservation in alcohol, and that 200 mm SL fish lost 1% and 300 mm fish lost 2% on average, he apparently did not try to compensate for this loss in length and apparently did not measure corresponding changes in body depth at the pelvic fins. Some of his material had been preserved much longer than several months and may have been even less representative of fresh material—the Olyutorskii Bay and Commander Island specimens were collected by A. P. Andriyashev in 1932 and 1950-52, indicating probable 9-30 yr storage in alcohol before measurement.

CONCLUSIONS

Because geographic variation was expressed in all parts of the morphology of Pacific ocean perch that I investigated, I conclude that the variation pervades body growth in the species. Over the eastern Bering Sea and eastern Pacific Ocean, adult measurements usually vary as V-shaped clines. Here, representatives of the same SL from the extremes of the sampling range (Vancouver Island and the eastern Bering Sea) resemble each other more than they resemble fish from near the midrange (Kodiak and Yakutat regions), where measurements often are smallest.

Only measurements of belly size and neighboring parts of the body have single, monotonic clines over the regions. Belly size increases dramatically from Vancouver Island to the eastern Bering Sea accompanied by corresponding size decreases in neighboring body measurements. The anterior and posterior boundaries of the belly, pelvic girdle (given by pelvic insertion), and anal-fin spines (given by body-depth anal) move relationally farther apart to give progressively larger bellies in populations farther from Vancouver Island and closer to the Bering Sea. Length of the spinous dorsal fin generally increases from southeast to northwest and length of the nape decreases, both apparently because of a relationally forward shift in the anterior insertion of the dorsal fin.

Nearly all morphometric characters apparently grow allometrically in Pacific ocean perch, but average body form does not change markedly with growth because allometric coefficients of most characters are near unity. Often, measurements vary between apparent slight but significant positive and negative allometry, depending on the sampling region. The symphyseal knob and 3d anal-fin spine (allometric coefficients were 1.52 and 0.73, respectively, including both sexes)

may be sufficiently allometric for the symphyseal knob to seem exceptionally prominent and the 3d anal-fin spine exceptionally small in some large specimens.

Most body dimensions average smaller in females than in males, but bellies are larger in females. The same mechanism, opposing relational movements of the pelvic girdle and the anal-fin spines, is responsible for sexual and geographic variation in belly size. Although sexual dimorphism increases with growth, sexual differences are not prominent and have broadly overlapping distributions. As a result, sexes probably cannot be reliably identified by gross examination of any of the 18 characters.

Neither geographic nor sexual variation is quantitatively similar between measurements in Pacific ocean perch—characters tend to vary with their absolute size. Overall, geographic variation is most poorly discriminated by the measurements of the 3d anal-fin spine, symphyseal knob, and 6th spinous ray in dorsal fin, and best discriminated by the belly, hind-trunk ventral, and head. Sexual dimorphism is most poorly discriminated by the measurements of the hind-trunk dorsal, spinous dorsal-fin length, and body-depth pelvic, and best discriminated by the belly, hind-trunk ventral, and pelvic insertion. Measurements that have been used for taxonomy of Pacific ocean perch in the past are relatively poor discriminators of geographic variation or possible genetic stocks or subspecies. Although body form changes significantly with geographic region, sex, and growth, differences are too small and unexplained variation too large for differences to be of value for distinguishing single specimens geographically.

Because of questions concerning validity and importance of published morphological information supporting supposed subspecies of Pacific ocean perch, it seems prudent that further claims for subspecies based on morphology be postponed until variation is reliably assessed over the entire species' range and definitive characteristics are known to be genetically based.

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GENETIC VARIATION IN CHINOOK, *ONCORHYNCHUS TSHAWYTSCHA*, AND COHO, *O. KISUTCH*, SALMON FROM THE NORTH COAST OF WASHINGTON

R. R. REISENBICHLER[1] AND S. R. PHELPS[2]

ABSTRACT

We used starch-gel electrophoresis to genetically characterize the populations of chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, in the major drainages of the north coast of Washington (the Quillayute, Hoh, Queets, and Quinault Rivers). Of 55 loci examined for electrophoretically detectable variation, 6 were polymorphic (frequency of the common allele was less than 0.95) in chinook salmon and 3 in coho salmon. Statistical tests of interdrainage and intradrainage variation for coho salmon were tenuous because most of the fish examined were from a single year class so that we could not account for variation among year classes. Nevertheless, these tests suggested that distinct stocks of coho salmon exist within drainages, and that variation was not significantly greater among drainages than within drainages. Interdrainage variation for wild chinook salmon was not significant. The data suggested that summer chinook salmon were electrophoretically different from fall chinook salmon, and the hatchery populations of chinook salmon were distinct from wild fish. A hatchery population developed primarily from north coast fish was electrophoretically more similar to wild chinook salmon than were the others.

Effective conservation and management of natural organisms require protection of the genetic resources (genes, gene combinations, gene pools) of these organisms (Altukhov 1981; Frankel 1983). Conservation of anadromous salmonids from the north coast of Washington (the area from the Quinault River to the Strait of Juan de Fuca) is receiving national attention because many of these fish spawn or rear in Olympic National Park, and the United States Congress has directed that the natural resources of National Parks be conserved. Olympic National Park is the only natural area administered by the National Park Service outside Alaska with substantial numbers of native anadromous salmonids. There is also international concern for conservation of natural (including genetic) resources in Olympic National Park, as indicated by inclusion of the park in the International Biosphere Reserve Program (Franklin 1977).

The present study was initiated to genetically characterize the populations of chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, from the major drainages of the north coast: the Quillayute, Hoh, Queets, and Quinault Rivers (Fig. 1). Coho salmon from two other streams in northwestern Washington (the Snohomish River and Snow Creek) and chinook salmon from Elwha Hatchery and the Wynoochee River were also sampled to enhance our perspective for examining north coast fish. Chinook and coho salmon are native to the west coast of North America from California to Alaska (Scott and Crossman 1973) and are the only species of Pacific salmon that are abundant in each of the major north coast drainages. Starch-gel electrophoresis was used to genetically characterize the fish.

Our objectives were 1) to develop a baseline set of allele frequency data; 2) to determine whether allele frequencies varied among major drainages; 3) to determine the degree of genetic structuring in coho salmon within major drainages; 4) to determine whether summer chinook salmon are electrophoretically distinct from fall chinook salmon; and 5) to determine whether hatchery populations of chinook salmon are electrophoretically distinct from wild (i.e., naturally spawned) fish.

We could not examine genetic structuring in chinook salmon within major drainages because wild adults were sampled in the lower portions of the rivers and thus their destinations within the major drainages were unknown, and samples of

[1]U.S. Fish and Wildlife Service, Seattle National Fishery Research Center, Building 204, Naval Station, Seattle, WA 98115.
[2]U.S. Fish and Wildlife Service, Seattle National Fishery Research Center, Building 204, Naval Station, Seattle, WA 98115; present address: Washington Department of Fisheries, Room 115, General Administration Building, Olympia, WA 98504.

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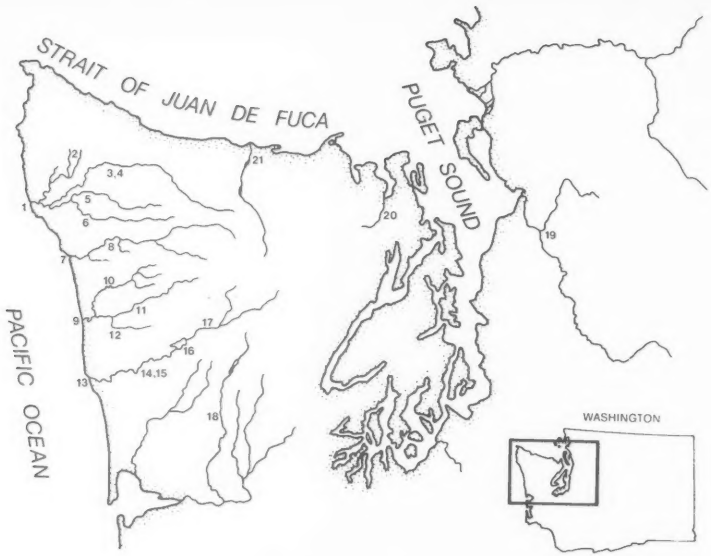


FIGURE 1.—Study area in northwestern Washington. This study focused on the four major stream systems of the north coast: the Quillayute (1), Hoh (7), Queets (9), and Quinault (13) drainages. Numbers identify sampling areas ("nets" indicates that adults were taken in the Indian gill net fisheries): (1) Quillayute River (nets); (2) Dickey River; (3) Soleduck River; (4) Soleduck Hatchery; (5) Calawah River; (6) Bogachiel River; (7) Hoh River (nets); (8) Hoh River; (9) Queets River (nets); (10) Clearwater River; (11) Upper Queets River, i.e., above the Salmon River; (12) Salmon River; (13) Quinault River (nets); (14) Lower Quinault River, i.e., below Lake Quinault; (15) Quinault National Fish Hatchery; (16) Quinault pens; (17) Upper Quinault River, i.e., above Lake Quinault; (18) Wynoochee River; (19) Snohomish River; (20) Snow Creek; (21) Elwha Hatchery.

wild juveniles contained unknown proportions of fish from genetically distinct runs.

MATERIALS AND METHODS

Three "runs" of chinook salmon and two runs of coho salmon occur in the study area. The runs are primarily distinguished by the time of year when the fish return to fresh water as adults. In general, spring chinook salmon return to fresh water from March to early June, summer chinook salmon from late June to August, and fall chinook salmon from mid-September to November. Similarly, summer coho salmon return to fresh water during August and early September, and fall coho salmon return from mid-October through November. Spring chinook salmon and summer coho salmon were not included in this study because returns to fresh water were low and few of these fish were available during our study. Adult salmon spawn in the autumn, and juveniles emerge from the gravel during the following winter or spring. Juvenile chinook salmon typically remain in the streams for several weeks to several months after emerging from the gravel, and enter the ocean during the summer or autumn; juvenile coho salmon remain in the streams for a year and enter the ocean during the spring.

Almost all summer coho salmon in the study area spawn in the Soleduck River (Quillayute River system) above Salmon Cascades (Houston 1983[3]). Our samples of fall-run juvenile coho salmon for the Soleduck River were taken from tributaries below Salmon Cascades to reduce the chance of including summer-run fish.

In addition to the fish rearing in streams,

[3]Houston, D. B. 1983. Andromous fish in Olympic National Park: a status report. Unpubl. rep. U.S. National Park Service, Port Angeles, WA.

salmon are raised in one federal, one state, and two tribal hatcheries along the north coast. Samples were taken from six hatchery populations (Table 1).

Table 1.—Run times and stock origins for hatchery populations used in genetic characterization.

Species of salmon	Run	Hatchery	Stock origin[1]
Chinook	Fall	Quinault National Fish Hatchery (Quinault NFH)	Quinault River and transfers from Hoh and Queets Rivers, and University of Washington, Willapa, Nemah, Finch Creek, Deschutes, Green River, and Samish Hatcheries.
Chinook	Fall	Quinault Tribal Penned Rearing Facility (Quinault Pens)	Queets River and transfers from Quinault, Green River, Samish, and Deschutes Hatcheries.
Chinook	Fall	Washington Department of Fisheries Soleduck Hatchery	Primarily Soleduck River; some transfers from Dungeness Hatchery.
Chinook	Spring-summer	Washington Department of Fisheries Soleduck Hatchery	Soleduck River and transfers from Dungeness, Cowlitz, and Umpqua Hatcheries.
Coho	Fall	Quinault NFH	Transfers from Quilcene, Purdy Creek, Moclips, Willapa, Soleduck, Simpson, Skagit, Green River, Hood Canal, and Cowlitz Hatcheries.
Coho	Fall	Washington Department of Fisheries Soleduck Hatchery	Primarily Soleduck River; some transfers from Dungeness Hatchery.

[1]From Houston (see text footnote 3).

Sample Collection

Fish were collected during 1983 from the 21 areas identified in Figure 1 (some juvenile chinook salmon were also available from collections made in 1982). Juvenile fish at hatcheries were collected with dip nets at several locations along each raceway containing the fish to be studied. Juveniles in streams were collected by trapping, electrofishing, and seining. A few juvenile coho salmon (usually <15 in each age group) were taken from each of several sites throughout each drainage. Juvenile chinook salmon were taken from several sites in the lower portions of the rivers. Juveniles of both species were collected from areas where no hatchery fish were released or before hatchery fish were released; they were either kept alive or held on ice for up to 8 hours and then frozen at −10°C or −70°C until thawed for electrophoretic analysis.

Samples of tissue from eye, liver, white muscle, and heart were taken from adult fish spawned at hatcheries or caught in gill net fisheries at the mouths of the rivers. At the hatcheries, samples of tissue were taken within 3 hours after the fish were killed for spawning. Adults from the fisheries were not available to us until they had been delivered to wholesale fish buyers. Some fish were delivered more than a day after the fish were killed; although most were kept on ice or refrigerated during this interval, some isozyme activity was lost. Tissue samples from all adults were placed on ice within 30 minutes after excision and were frozen at −10°C or −70°C within 6 h.

Electrophoresis

We used horizontal starch-gel electrophoresis (Utter et al. 1974; May et. al. 1979) to assay fish tissues. Eye, heart, liver, and muscle tissues were removed from partly thawed juveniles just before electrophoretic analysis. We identified alleles at loci encoding specific enzymes, using the staining methods of Harris and Hopkinson (1976) and Allendorf et al. (1977). The nomenclature used to describe the gene loci and the allele variants followed Allendorf and Utter (1979).

Of the 40 enzymes examined, 30 had sufficient activity and resolution to be used in this study

(Table 2). Initially all 30 enzymes were examined in all fish; in later samples, however, we omitted the loci in chinook salmon that had been determined to be monomorphic in previous studies or in our initial screening.

TABLE 2.—Enzymes and loci examined in chinook and coho salmon. Enzyme commission numbers are in parentheses. Tissue E refers to eye, H to heart, L to liver, and M to white muscle. Buffer system 1 was described by Ridgway et al. (1970), 2 by Clayton and Tretiak (1972), and 3 by Markert and Faulhaber (1965) and Kobayashi et al. (1984).

Enzyme	Chinook salmon			Coho salmon		
	Loci	Tissue	Buffer	Loci	Tissue	Buffer
β-N-Acetyl-galactosaminidase (3.2.1.23)	[1]*bGala-2*	L	2	[1]*bGala-1*	L	2
				bGala-2	L	2
N-Acetyl-B-glucosaminidase (3.2.1.30)	[1]*bGa-1*	L	1	[1]*bGa-1*	L	1
Acid phosphatase (3.1.3.2)	[1]*Acp-1*	L	2	[1]*Acp-1*	L	2
	[1]*Acp-2*	L	2	[1]*Acp-2*	L	2
Aconitate hydratase (4.2.1.3)	[1]*Ah-1*	H	2	[1]*Ah-1*	H	2
	[1]*Ah-2*	H	2	[1]*Ah-2*	H	2
	Ah-3	L	2	*Ah-3*	L	2
Adenosine deaminase (3.5.4.4)	—	—	—	[1]*Ada-1*	M	1,3
				Ada-2	M,E	1,3
Adenylate kinase (2.7.4.3)	[1]*Ak-1*	M	2	[1]*Ak-1*	M	2
Alanine aminotransferase (2.6.1.2)	[1]*Alat-1*	M	1	[1]*Alat-2*	M	1
Alcohol dehydrogenase (1.1.1.1)	*Adh-1*	L	2	[1]*Adh-1*	L	2
Aspartate aminotransferase (2.6.1.1)	[1]*Aat-1*	L	2	[1]*Aat-1,2*	L	2
	[1]*Aat-3,4*	M	2	*Aat-3,4*	M	2
	[1]*Aat-5*	E	2	[1]*Aat-5*	E	2
Creatine kinase (2.7.3.2)	[1]*Ck-1*	M	1	*Ck-1*	M	1
	[1]*Ck-2*	M	1	[1]*Ck-2*	M	1
	[1]*Ck-3*	M	1	[1]*Ck-3*	M	1
Diaphorase-NADH (1.6.*.*)	[1]*Dia-1*	L	1	[1]*Dia-1*	L	1
Diaphorase-NADPH (1.6.*.*)	[1]*DiaP-1*	L	1	[1]*DiaP-1*	L	1
Fructose bisphosphate aldolase (4.1.2.3)	[1]*Fbald-1*	E	2	[1]*Fbald-1*	E	2
	[1]*Fbald-2*	E	2	[1]*Fbald-2*	E	2
Fumarate hydratase (4.2.1.2)	[1]Fh-1	M	1	[1]*Fh-1*	M	1
Glucose-6-phosphate isomerase (5.3.1.9)	[1]*Gpi-1*	M	1	*Gpi-1*	M	1
	Gpi-2	M	1	*Gpi-2*	M	1
	Gpi-3	M	1	*Gpi-3*	M	1
β-Glucuronidase (3.2.1.31)	[1]*bGus-1*	L	1	[1]*bGus-1*	L	1
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	[1]*Gapdh-3*	E	2	[1]*Gapdh-3*	E	2
	[1]*Gapdh-4*	E	2	[1]*Gapdh-4*	E	2
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	[1]*G3pdh-1*	M	2	*G3pdh-1*	M	2
	[1]*G3pdh-2*	M	2	[1]*G3pdh-2*	M	2
	[1]*G3pdh-3,4*	H	2			
L-Iditol dehydrogenase (1.1.1.14)	*Iddh-1,2*	L	1	—	—	—
Isocitrate dehydrogenase (1.1.1.42)	[1]*Idh-1*	M	2	[1]*Idh-1*	M,H	2
	Idh-2	M	2	[1]*Idh-2*	M,H	2
	Idh-3,4	M,L	2	*Idh-3,4*	L,H	2
L-Lactate dehydrogenase (1.1.1.27)	[1]*Ldh-1*	M	1	[1]*Ldh-1*	M	1
	[1]*Ldh-2*	M	1	[1]*Ldh-2*	M	1
	[1]*Ldh-3*	E	1	*Ldh-3*	E	1
	[1]*Ldh-4*	L	1	*Ldh-4*	L	1
	[1]*Ldh-5*	E	1	[1]*Ldh-5*	E	1
Lactoylglutathione lyase (4.4.1.5)	[1]*Lgl-1*	E,M	1	*Lgl-1*	E,M	1
Malate dehydrogenase (1.1.1.37)	*Mdh-1,2*	L	2	*Mdh-1,2*	L	2
	Mdh-3,4	M	2	*Mdh-3,4*	M	2
Malate dehydrogenase (NADP+) (1.1.1.40)	[1]*MdhP-1*	M	2	*MdhP-1*	M	2
	[1]*MdhP-2*	M	2	[1]*MdhP-2*	M	2
	[1]*MdhP-3*	L	2	[1]*MdhP-3*	L	2
Mannose-6-phosphate isomerase (5.3.1.8)	*Mpi-1*	E	2	*Mpi-1*	E	2
α-Mannosidase (3.2.1.24)	[1]*aMan-1*	L	1	[1]*aMan-1*	L	1
Phosphoglucomutase (5.4.2.2)	*Pgm-1*	M	1	[1]*Pgm-1*	M	2
				Pgm-2	M	2
Phosphogluconate dehydrogenase (1.1.1.44)	*Pgdh-1*	M	2	*Pgdh-1*	M	2
Phosphoglycerate kinase (2.7.2.3)	[1]*Pgk-1*	M	2	[1]*Pgk-1*	M	2
	Pgk-2	M	2	[1]*Pgk-2*	M	2
Superdioxide dismutase (1.15.1.1)	*Sod-1*	L,H	1	[1]*Sod-1*	L	1,2
	[1]*Sod-2*	L	2			

[1]No isozyme variation observed.

Data Analysis

Goodness-of-Fit Tests

We used the chi-square test to examine genotype frequencies for deviation from the (Hardy-Weinberg) proportions expected with random mating. Cells with an expected number <5 were combined with the next larger cell. The significance level for each test was modified to account for the increase in type I error when multiple tests of the same hypothesis are made (Cooper 1968). Tests were considered significant if the chi-square statistic exceeded the critical value for chi-square associated with a probability of $0.05/n$, where n was the number of loci tested within a sample. In this way the overall probability of rejecting H_0 by chance alone was approximately $1 - (1 - 0.05/n)^n \cong 0.05$ for each sample. Genotypes for *Idh-3,4*, *Mdh-1,2*, and *Mdh-3,4* were not tested because these systems consisted of pairs of loci with identical electrophoretic mobility, and genotypes at each locus could not be determined.

The likelihood ratio test (G-test; Sokal and Rohlf 1981) was used to test equality in allele frequencies between year classes. Here also, cells with an expected number <5 were combined with the next largest cell. The G-statistics, summed over all loci, were considered significant if they exceeded the critical value for chi-square associated with a probability of $0.05/s$, where s was the number of samples tested. Samples from streams and samples from hatcheries were tested as separate groups. The correction for multiple comparisons was made because each of the three H_0—no interbrood variation by drainage, by streams within drainages, or by hatchery—was independently tested for several drainages, streams, or hatcheries, respectively.

Analysis of Variance

We used analysis of variance (ANOVA) to test interdrainage differences, differences between hatchery and wild chinook salmon, and differences between summer and fall runs of chinook salmon. Data for coho salmon were not tested by ANOVA because data were available for only one year class from most locations, and estimates of interbrood variation in allele frequencies would have come from only two sample locations. The data used were from the loci scored for fish from each major north coast drainage and with frequencies <0.95 for the common (100) allele. The values used in the analysis were the arcsin of the square root of the frequency of the common allele at each locus. Differences were tested by contrasts (Table 3) or by partitioning the sum of squares within a one-way ANOVA for each locus (Snedecor and Cochran 1967; SPSS, Inc. 1983). Groups included in this analysis were as follows (adults would have spawned in 1983):

Cell	*Group*	*Run*	*Replicate*
1	Quillayute River	Mixed	1981 brood
			1982 brood
2	Hoh River	Mixed	1981 brood
			1982 brood
3	Queets River	Mixed	1981 brood
			1982 brood
4	Quinault River	Mixed	1981 brood
			1982 brood
5	Wynoochee River	Mixed	1982 brood
6	Quinault Pens	Fall	1982 brood
7	Quinault NFH	Fall	1981 brood
			1982 brood
8	Soleduck Hatchery	Fall	1981 brood
			1982 brood
9	Hoh River	Fall	Adults
10	Queets River	Fall	Adults
11	Soleduck Hatchery	Spring-summer	(data from Milner et al. 1983[1])
			1982 brood
			Adults
12	Hoh River	Summer	Adults
13	Queets River	Summer	Adults

[1]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. Rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

Juveniles from the different runs of chinook salmon were morphologically indistinguishable and our estimates of error variance were probably inflated because they were based on samples (of juveniles) that vary from year to year in the proportion of fish from each race. As a result, the (discriminatory) power for detecting differences between groups was impaired. In view of this reduced discriminatory power, differences with $0.05 \leq P < 0.1$ were noted in the text; statistical significance, however, was reserved for differences with $P < 0.05$.

Adult fall and summer chinook salmon from the Quillayute River and adult fall chinook salmon from the Quinault River were not included in the ANOVA because adults returning to these streams include large numbers of hatchery fish (Houston fn. 3). Adult summer chinook

TABLE 3.—Chinook salmon—coefficients for contrasts (Snedecor and Cochran 1967) within the analysis of variance. Cell numbers refer to groups identified in text. Within each contrast, the mean allele frequencies for groups with positive coefficients were compared with the mean frequencies for groups with negative coefficients.

	Cell												
Contrast	1	2	3	4	5	6	7	8	9	10	11	12	13
Interdrainage variation													
1 Fall-run adults	0	0	0	0	0	0	0	0	−1	1	0	0	0
2 Summer-run adults	0	0	0	0	0	0	0	0	0	0	0	−1	1
Hatchery vs. wild													
3 Summer run	0	0	0	0	0	0	0	0	0	0	−2	1	1
Fall run:													
4 Quinault Pens	0	0	0	0	0	−2	0	0	1	1	0	0	0
5 Quinault NFH	0	0	0	0	0	0	−2	0	1	1	0	0	0
6 Soleduck Hatchery	0	0	0	0	0	0	0	−2	1	1	0	0	0
Summer vs. fall													
7 Adults	0	0	0	0	0	0	0	0	−1	−1	0	1	1

salmon from the Quinault River were not included because many hatchery fall chinook salmon return to the Quinault River with the summer-run salmon (during August, when most of our sampling was done) and our samples probably included a high proportion of fall-run hatchery fish (Larry Gilbertson[4]).

Gene Diversity Analysis

We used a modification of Chakraborty's (1980) gene diversity analysis to examine the hierarchical structure of genic diversity among the samples of wild coho salmon from the north coast. This analysis partitions total gene diversity (H_t, heterozygosity of allele frequencies over locations) into interdrainage and intradrainage components (Nei 1973). We considered three levels of population subdivision (Fig. 2)—broods (b), streams within drainages (w), and drainages (d)—so that $H_t = H_s + D_{bw} + D_{wd} + D_{dt}$, where H_s is the average heterozygosity within samples, D_{bw} is the gene diversity between broods, D_{wd} is the diversity within drainages, and D_{dt} is the diversity among drainages. Relative gene diversities (G_{ij}) are the proportions of H_t associated with a particular hierarchical level; for example, $G_{wd} = D_{wd}/H_t$.

[4] Larry Gilbertson, Quinault Tribal biologist, Quinault Indian Nation, P.O. Box 189, Taholah, WA 98587, pers. commun. August 1983.

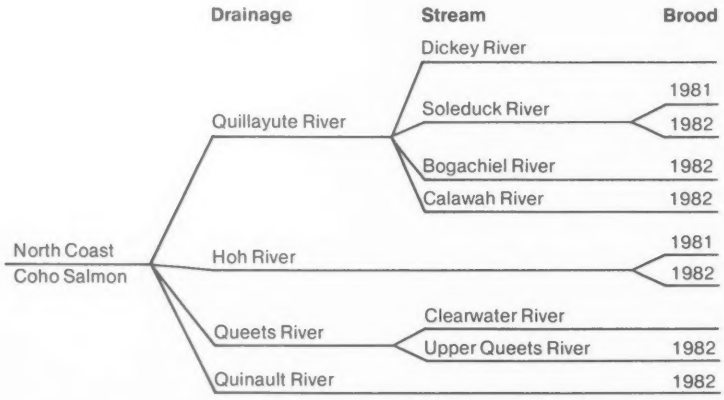


FIGURE 2.—Coho salmon—hierarchical subdivisions used in the gene diversity analysis for wild fish from the north coast of Washington (see test). Where brood is not identified, fish were from both the 1981 and 1982 broods.

The modification to Chakraborty's (1980) analysis consisted of giving equal weight to subgroups within a cell, rather than weighting them according to the number of samples within each subgroup. Our sampling design did not include all possible or desirable subgroups; the design was a compromise that allowed us to evaluate the different levels of subdivision and still remain within our budget. We felt that equal weighting was necessary because the number of subgroups within a cell usually did not reflect the "true" number of subgroups that may have existed for that cell. Donald Campton (University of Florida, Gainesville) provided a computer program, coded in Fortran 77, that included the required modification to Chakraborty's equations.

Cluster Analysis

The unweighted pair group method of cluster analysis (UPGM analysis; Sneath and Sokal 1973) and (nonmetric) multidimensional scaling (Gordon 1981; Kruskal and Wish 1977) were used to illustrate genetic similarities among samples. These two cluster analyses were applied to values of Nei's (1972) genetic distance calculated for each pair of samples. Data from the separate broods were pooled with equal weight for these analyses.

RESULTS

Chinook Salmon

Although fish from two locations showed significant deviation from Hardy-Weinberg proportions ($P < 0.05/n_i$ where n_i was the number of loci tested for location i)—juveniles of the 1982 brood from the Bogachiel River were deficient in heterozygotes at the *Pgk-2* locus and juveniles of the 1982 brood from the Hoh River had an excess of heterozygotes at the *Gpi-2* locus—these deviations are probably spurious, given the large number (20) of samples tested.

Interbrood variation in allele frequencies was significant ($P < 0.01$) for wild fish and for hatchery fish (Table 4). Six loci, or pairs of loci, showed sufficient variation and were scored for enough fish ($n > 25$) to be used in the ANOVA (Fig. 3, App. Table 1). Variation between drainages was not significant, although summer-run fish may differ between drainages ($P = 0.07$, Table 4). Hatchery fish were different from wild fish (contrasts 3 to 6 in Table 5).

The UPGM cluster analysis showed that the hatchery populations were distinct from wild juveniles and from all but one (Quinault River) sample of adults (Fig. 4). Of the hatchery populations, fall-run fish from Soleduck Hatchery were

TABLE 4.—Chinook salmon—likelihood ratio analysis of interbrood variation at 10 codominant loci. Significant levels were evaluated for totals only. G = likelihood ratio statistic.

	Ah-3		*Gpi-2*		*Idh-3,4*		*Mdh-3,4*		*Mpi-1*		*Pgm-1*		*Pgk-2*		*Sod-1*		Total	
	df	G	df	G	df	G	df	G	df	G	df	G	df	G	df	G	df	G
Interbrood variation for drainages																		
Quillayute River	1	1.36	—	—	1	15.61	1	6.26	1	0.25	1	0.00	1	3.90	1	3.63	7	31.01**
Hoh River	2	2.66	—	—	1	10.21	—	—	1	1.78	1	3.22	1	0.09	1	0.21	7	18.16*
Queets River	1	0.00	—	—	1	0.05	—	—	1	2.73	1	0.19	1	1.12	1	0.32	6	4.41
Group total																	20	53.58†
Interbrood variation for streams (within drainages)																		
Soleduck River	1	4.77	—	—	—	—	—	—	1	1.83	1	0.65	1	4.79	1	3.85	5	15.89*
Bogachiel River	1	0.20	—	—	—	—	1	5.81	1	0.33	1	0.44	1	0.55	1	0.81	6	8.14
Hoh River	2	2.66	—	—	1	10.20	—	—	1	1.78	1	3.22	1	0.08	1	0.21	7	18.16*
Queets River above Salmon River	1	0.42	—	—	1	2.58	—	—	1	3.64	1	16.55	1	2.22	1	0.34	6	25.76**
Clearwater River	1	0.43	—	—	1	2.73	—	—	1	0.57	1	6.57	1	0.07	1	0.02	6	10.39
Group total																	30	78.34†
Interbrood variation for hatcheries																		
Soleduck Hatchery																		
Spring/summer	2	1.98	1	0.29	2	6.46	—	—	2	9.56	—	—	2	4.45	2	12.58	11	35.31**
Fall	1	2.26	—	—	—	—	—	—	1	0.89	—	—	—	—	1	0.31	3	3.46
Quinault NFH (Fall)	1	1.63	—	—	1	5.99	—	—	1	9.53	1	2.21	1	11.41	1	1.29	6	32.06**
Elwha Hatchery	—	—	1	9.58	—	—	—	—	1	2.28	—	—	1	7.15	1	0.30	4	19.34**
Group total																	24	90.17†

*$P < 0.05/n$ } where $n = 3$ for interbrood variation within drainages, $n = 5$ for variation within streams, and $n = 4$ for variation within hatcheries. These are corrections for multiple comparisons (Cooper 1968).
**$P < 0.01/n$ }
†$P < 0.01$.

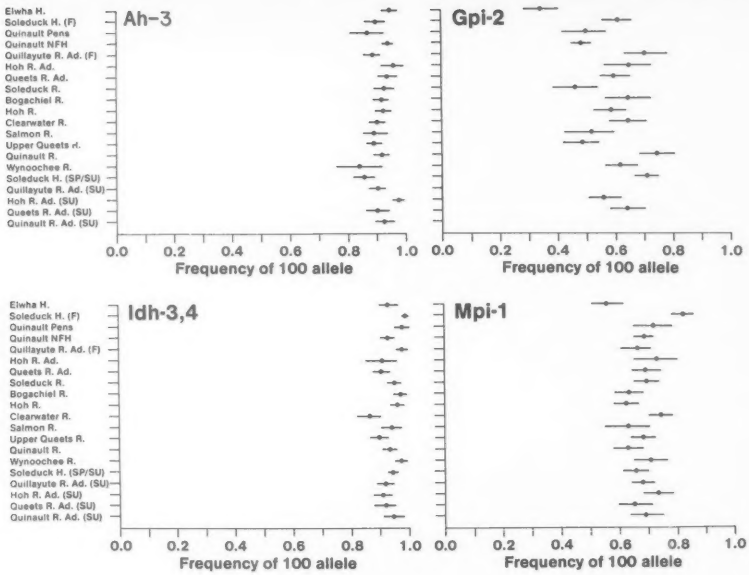


FIGURE 3a.—Chinook salmon—common-allele frequencies (q) for four protein-coding loci, or pairs of loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not presented and were not used in the analyses. Data for Gpi-2 were not included in the ANOVA because of missing data (see Appendix Table A1). H. = hatchery; Ad. = adults; F = fall run; SP/SU = mixed spring/summer run; SU = summer run. Adults were from the fall run unless specified otherwise.

TABLE 5.—Chinook salmon—results from multivariate (MANOVA) and univariate analyses of the variance among frequencies (q) of the 100 allele at each of six loci or pairs of loci. Actual values in the analyses were transformed frequencies: arcsin $\sqrt{q}$. Hypothesis numbers correspond to those in the text table for contrasts under Materials and Methods. F = F statistics, df = degrees of freedom for the F statistics.

Hypothesis	*P* value from MANOVA		Tests at individual loci					
			Ah-3	*Idh-3,4*	*Mpi-1*	*Pgm-1*	*Pgk-2*	*Sod-1*
Interdrainage variation								
1 Fall run adults	0.54	F	0.15	0.00	0.14	0.52	0.27	0.18
		df	1,7	1,7	1,7	1,7	1,7	1,7
2 Summer run adults	0.07	F	5.39	0.00	0.51	0.00	1.00	0.14
		df	1,7	1,7	1,7	1,7	1,7	1,7
Juveniles	—	F	0.43	1.45	0.54	0.38	0.85	0.31
		df	3,6	3,7	3,7	3,7	3,7	3,6
Hatchery vs. wild								
3 Summer run	0.34	F	11.46	0.54	0.44	22.15*	0.28	5.67
		df	1,7	1,7	1,7	1,7	1,7	1,7
Fall run								
4 Quinault Pens	0.03*	F	4.93	1.50	0.00	0.06	4.40	0.18
		df	1,7	1,7	1,7	1,7	1,7	1,7
5 Quinault NFH	0.06	F	0.18	0.33	0.09	0.53	8.91	7.45
		df	1,7	1,7	1,7	1,7	1,7	1,7
6 Soleduck Hatchery	0.03*	F	6.06	4.37	2.79	11.44	0.00	2.84
		df	1,7	1,7	1,7	1,7	1,7	1,7
Summer vs. fall								
7 Adults	0.06	F	0.00	0.05	0.10	1.32	1.71	0.67
		df	1,7	1,7	1,7	1,7	1,7	1,7

*$P < 0.05$ for MANOVA, or $P < 0.05/6$ for univariate tests.

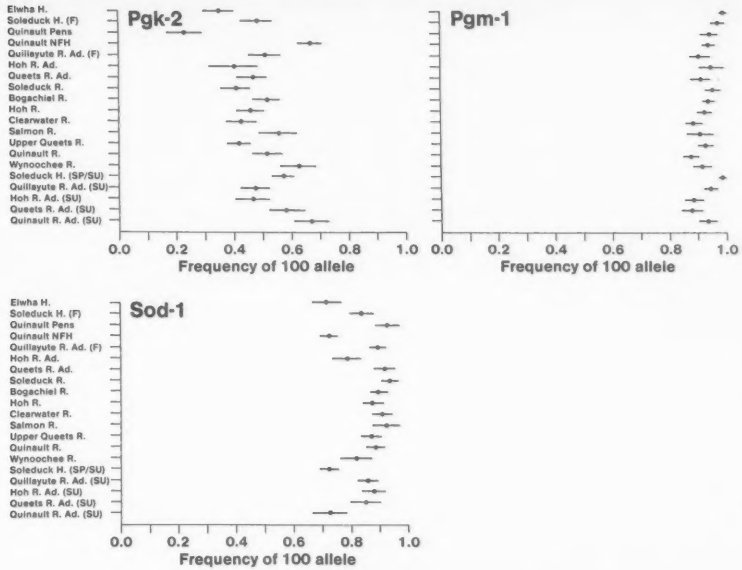
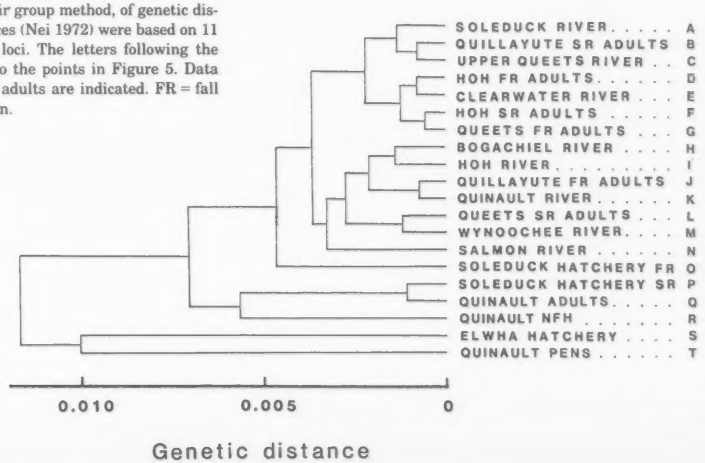


FIGURE 3b.—Chinook salmon—common-allele frequencies (q) for three protein-coding loci, or pairs of loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not presented and were not used in the analyses. Data for Gpi-2 were not included in the ANOVA because of missing data (see Appendix Table A1). H. = hatchery; Ad. = adults; F = fall run; SP/SU = mixed spring/summer run; SU = summer run. Adults were from the fall run unless specified otherwise.

FIGURE 4.—Chinook salmon—dendrogram showing results of analysis, by the unweighted pair group method, of genetic distance between samples. Distances (Nei 1972) were based on 11 protein-coding loci or pairs of loci. The letters following the names of samples correspond to the points in Figure 5. Data were from juvenile fish unless adults are indicated. FR = fall run; SR = spring or summer run.


SOLEDUCK RIVER . . . . . A
QUILLAYUTE SR ADULTS B
UPPER QUEETS RIVER . . C
HOH FR ADULTS . . . . . D
CLEARWATER RIVER . . . E
HOH SR ADULTS . . . . . F
QUEETS FR ADULTS . . . G
BOGACHIEL RIVER . . . . H
HOH RIVER I
QUILLAYUTE FR ADULTS J
QUINAULT RIVER . . . . . K
QUEETS SR ADULTS . . . L
WYNOOCHEE RIVER. . . . M
SALMON RIVER . . . . . N
SOLEDUCK HATCHERY FR O
SOLEDUCK HATCHERY SR P
QUINAULT ADULTS. . . . . Q
QUINAULT NFH . . . . . R
ELWHA HATCHERY . . . . S
QUINAULT PENS . . . . . T
0.010
0.005
0
Genetic distance

most similar to wild fish. Summer-run adults and fall-run adults from the Quillayute River both clustered with the wild fish, suggesting that a large proportion of the fish in these samples were wild fish. Multidimensional scaling gave similar results and more clearly illustrated that hatchery populations were distinct not only from the wild fish but also from each other (Fig. 5).

Coho Salmon

Coho salmon showed genic variability at 21 loci or pairs of loci; however, the frequency of the common allele was <0.95 for most samples at only 2 loci: *bGala-2* and *Idh-3,4* (Fig. 6, App. Table 2). Allendorf and Utter (1979) found a similar lack of variation, reporting that coho salmon display the least amount of electrophoretic variation of the five Pacific salmon species in North America.

Hierarchical analysis of genic diversity (heterozygosity) showed that the interbrood level accounted for 2% (= 0.09/(0.09 + 0.85 + 3.97; Table 6) of the genic diversity observed among samples of coho salmon; the within-drainage level accounted for 17% and the interdrainage level for 81%. Variation at *Pnp-1* had a substantial influence on the average locus values. Unfortunately, data for *Pnp-1* were missing for several of the samples because the methodology for this enzyme was not stabilized until we were well into our study. With *Pnp-1* excluded from the analysis, the interbrood level accounted for 5% of the genic diversity observed among samples, the within-drainage level accounted for 39%, and the interdrainage level accounted for 56%.

Variation in allele frequencies among streams within the Quillayute and Queets drainages was statistically significant (tested at *bGala-2, Idh-3,4*, and *Pnp-1*; $G = 11.27$ with 5 degrees of freedom; $P < 0.05$); however, interpretation of this result is complicated because data were not available to adequately account for variation among year classes. Variation among drainages was not significantly greater than variation within drainages ($P > 0.10$, hierarchical likelihood ratio

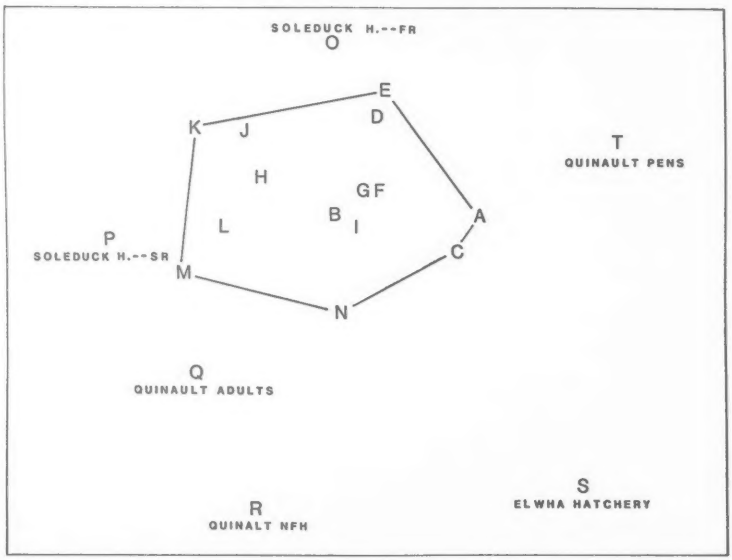


FIGURE 5.—Chinook salmon—two-dimensional representation (from multidimensional scaling) of genetic distances among samples collected for this study. The letters correspond to the groups identified in Figure 4. The polygon encloses the samples of wild fish (A through N). The aim of multidimensional scaling is to represent each group by a point in two-dimensional space so that the relative distances among points represent the relative (genetic) distances between groups.

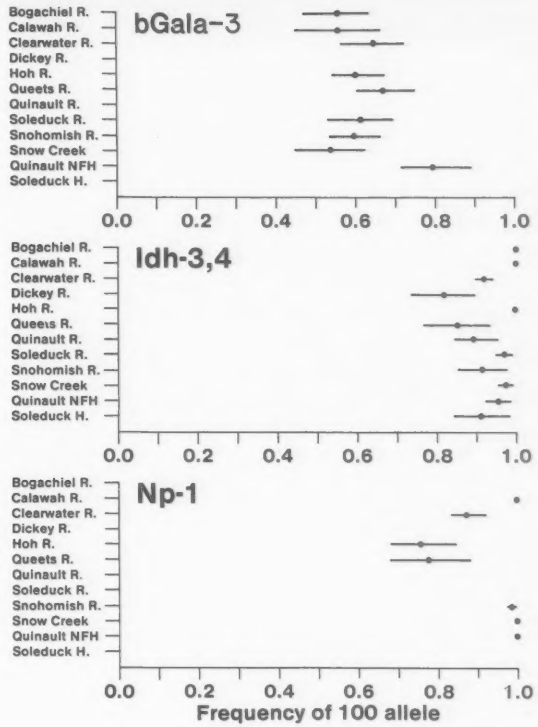


FIGURE 6.—Coho salmon—common-allele frequencies (q) for several protein-coding loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not shown and were not used in analysis.

TABLE 6.—Coho salmon—hierarchical analysis of electrophoretically detectable gene diversity for coho salmon from the Quillayute, Hoh, Queets, Quinault and Wynoochee Rivers. Analysis was based on 58 loci, including 36 that were monomorphic. The hierarchical design is shown in Figure 3.

Locus	Total gene diversity (H_T)	Relative gene diversity (%)			
		Within samples	Among broods	Within drainages	Among drainages
Average	0.021	95.09	0.09	0.85	3.97
Average excluding *Pnp-1*	0.016	97.64	0.12	0.93	1.31

analysis; Grant et al. 1980; Smouse and Ward 1978).

Samples without data for *bGala-1* or *Idh-3,4*, the most variable loci, were omitted from the UPGM cluster analysis (Fig. 7) and multidimensional scaling (Fig. 8). Both analyses showed that fish from Quinault NFH were distinct from wild fish; much of this distinctiveness occurred at the *bGala-2* locus (Fig. 6). Fish from Snow Creek and the Snohomish River clustered among the wild fish from the north coast. The results were similar when *Pnp-1* was excluded from the analysis, except that fish from the upper Queets River were no longer distinct from the other wild fish.

DISCUSSION

Wild Populations

Variation in allele frequencies among drainages for chinook salmon was not statistically significant. The inability to detect differences among drainages could have resulted from 1) low statistical power (probability of rejecting H_0 if it is false) because we had too few broods or because variation in racial composition of juveniles in different years inflated the estimates of error variance, 2) our exclusive reliance on data for genes that can be sampled by electrophoresis, or 3) a lack of true genetic difference among groups. We

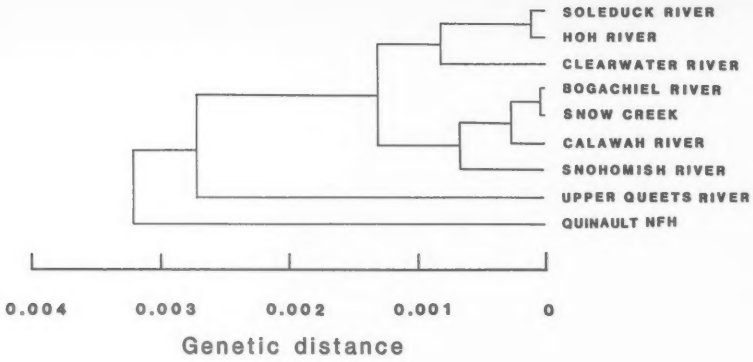


FIGURE 7.—Coho salmon—dendrogram showing results of analysis, by the unweighted pair group method, of genetic distance between samples. Distances were based on 24 protein-coding loci or pairs of loci.

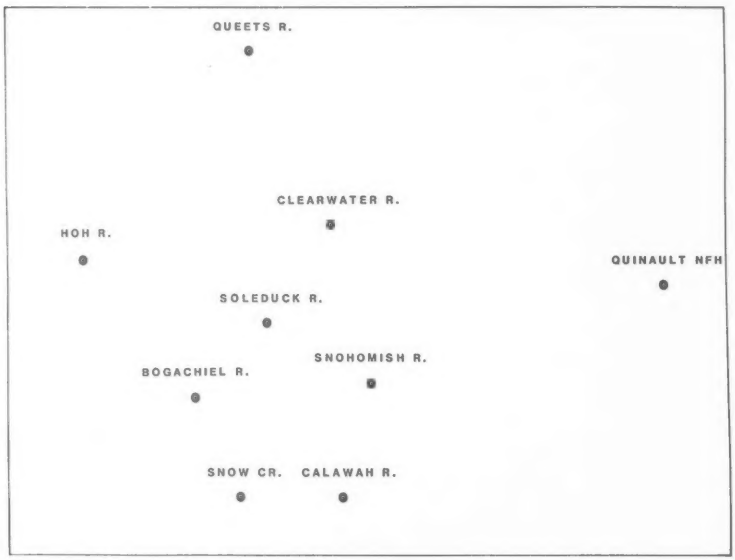


FIGURE 8.—Coho salmon—two-dimensional representation (from nonmetric multidimensional scaling) of genetic distances among samples collected for this study. Only samples scored for *bGala-2* and *Idh-3,4* were included in the analysis.

emphasize that the lack of differentiation in frequencies of electrophoretically detectable alleles does not preclude the existence of important genetic differences or status as separate stocks (genetic populations). The high degree of "homing" by both chinook salmon (see, e.g., Rich and Holmes 1928) and coho salmon (see, e.g., Shapavalov and Taft 1954) to the streams from which they originate suggests that salmon from different drainages should be considered as separate

stocks unless strong evidence exists to the contrary.

Our data suggested that summer chinook salmon were distinct from fall chinook salmon ($P = 0.06$, Table 5). Electrophoretic differences between distinct runs or life history types of chinook salmon were also found within the Nanaimo River system (Carl and Healey 1984) and within the Columbia River system (Kristiansson and McIntyre 1976). Summer-run fish from different streams along the north coast were not sufficiently similar to form a cluster separate from the fall-run fish (Figs. 4, 5), and the differences among populations of summer-run fish may be as great as the differences between summer- and fall-run fish. Unfortunately the small number of populations precluded rigorous comparison of these differences.

The (significant) variation in allele frequencies between year classes of juvenile chinook salmon may have been exaggerated by variation between years in the proportion of fish from the three different runs. This possibility illustrates the need for sampling adult chinook salmon (only adults can be distinguished according to run) in river systems where juveniles from different runs occur together. Of course, the utility of sampling adults to genetically describe wild populations is compromised if adult hatchery and wild fish occur together and cannot be reliably separated.

The gene diversity analysis for coho salmon showed that diversity within drainages was eight to nine times the diversity among broods, with or without *Pnp-1* included in the analysis, and suggested that separate breeding units exist within drainages as well as between drainages. Separate breeding units within drainages were also suggested by the likelihood ratio analysis.

Hatchery Fish Versus Wild Fish

Analysis of variance for hatchery and wild chinook salmon, and the cluster analyses for both chinook and coho salmon showed that the hatchery populations of the north coast were genetically distinct from the populations of wild fish. Indeed, coho salmon from Snow Creek or from the Snohomish River were more similar to wild coho salmon from the north coast than were coho salmon from Quinault National Fish Hatchery (Fig. 7).

The differences between hatchery and wild fish were to be expected because the hatchery populations were developed with fish from locations in addition to the local stream or exclusive of the local stream. Among chinook salmon, fall-run fish at Soleduck Hatchery were the most similar to wild fish (Fig. 5), probably because the Soleduck Hatchery population was the only hatchery population developed primarily with local fish (Houston fn. 3). Fall coho salmon at Soleduck Hatchery were also primarily developed with local fish but were not included in the analysis because of missing data. We would expect these coho salmon to be more similar to wild fish than were the coho salmon from Quinault National Fish Hatchery—and that expectation held for allele frequencies at *Ada-2* and *Ldh-4*, and was not countered by evidence from any other loci (App. Table A2).

It is reasonable to assume that interbreeding with fall chinook salmon (or fall coho salmon) from Soleduck Hatchery will cause less reduction of fitness and less genetic change for wild fish than will interbreeding with the other (less similar) hatchery fish (Helle 1981; Reisenbichler 1984). The observed differences between fall chinook salmon at Soleduck Hatchery and wild fish probably exist because few wild fish are included in the hatchery brood stock. Data for steelhead, *Salmo gairdneri*, (Reisenbichler and Phelps 1985[5]) illustrate that the continued use of wild fish in the hatchery brood stock and avoidance of selective breeding are necessary to maintain a hatchery population that is genetically similar to wild fish. Where hatchery populations can be managed separately from wild populations and where few hatchery fish stray onto natural spawning areas, perhaps there is little reason to ensure that hatchery fish are genetically similar to wild fish. However, where substantial numbers of hatchery fish successfully spawn in streams and where genetic resources are to be conserved, hatchery fish should be as genetically similar as possible to the wild fish (e.g., Helle 1981).

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[5]Reisenbichler, R. R., and S. R. Phelps. 1985. Genetic structure of steelhead, *Salmo gairdneri*, from the north coast of Washington State. Unpubl. rep. National Fishery Research Center, Seattle, WA.

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APPENDIX TABLE 1.—Allele frequencies for chinook salmon from Washington. Each allele is designated by its mobility (relative to the common allele) times 100. *N* is the number of fish scored for most loci; however, fewer fish may have been scored at some loci. Frequencies from fewer than *N*/2 fish are identified with an asterisk, and frequencies from fewer than 25 fish are not shown and were not used in our analyses. Numbers preceding sample names correspond to locations shown in Figure 1.

Location and sample	Brood	*N*	*Ah-3*				*Adh-1*		*Gpi-2*			
			100	85	118	108	−100	−50	100	67	−15	150
Quillayute River												
1 Fall-run adults	[1](1983)	99	0.892	0.097	0.011	—	0.990	0.010	0.714*	0.276*	0.010	—
1 Summer-run adults	[1](1983)	120	0.906	0.094	—	—	0.996	0.004	—	—	—	—
3 Soleduck River	1981	70	0.884	0.101	0.014	—	0.971	0.029	—	—	—	—
	1982	40	0.971	0.029	—	—	—	—	0.462	0.488	0.010	—
4 Soleduck Hatchery												
Fall run	[2]pre-1982		0.840	0.130	—	0.030	0.990	0.010	—	—	—	—
	1982	40	—	—	—	—	—	—	0.662	0.288	0.012	0.038
Spring/summery run	[2]pre-1982		0.850	0.150	—	—	0.980	0.020	—	—	—	—
	1982	50	0.830	0.170	—	—	1.000	—	0.700	0.300	—	—
	[1](1983)	77	0.889	0.111	—	—	1.000	—	0.761	0.239	—	—
6 Bogachiel River	1981	70	0.926	0.066	0.008	—	0.985	0.015	—	—	—	—
	1982	40	0.894	0.091	—	0.015	—	—	0.650	0.338	—	0.012
Hoh River												
7 Fall-run adults	[1](1983)	37	0.957	0.043	—	—	0.973	0.027	0.650	0.350	—	—
7 Summer-run adults	[1](1983)	86	0.983	0.017	—	—	0.960	0.040	0.574	0.426	—	—
8 Juveniles	1981	70	0.900	0.064	0.036	—	0.991	0.009	—	—	—	—
	1982	76	0.950	0.029	0.021	—	—	—	0.592	0.388	0.020	—
Queets River												
9 Fall-run adults	[1](1983)	94	0.944	0.044	0.012	—	0.978	0.022	0.595	0.399	0.006	—
9 Summer-run adults	[1](1983)	60	0.907	0.074	0.019	—	0.969	0.031	0.652	0.348	—	—
10 Clearwater River	1981	70	0.891	0.094	0.014	—	0.957	0.043	—	—	—	—
	1982	48	0.917	0.052	0.031	—	0.980	0.020	0.650	0.350	—	—
12 Salmon River	1982	48	0.880	0.109	0.011	—	0.943	0.057	0.531	0.469	—	—
11 Upper Queets River	1981	70	0.906	0.087	0.007	—	0.957	0.043	—	—	—	—
	1982	54	0.880	0.070	0.050	—	—	—	0.491	0.500	0.009	—
Quinault River												
13 Adults	[1](1983)	64	0.927	0.073	—	—	0.976	0.024	—	—	—	—
14 Lower Quinault River	1982	55	—	—	—	—	—	—	0.750	0.236	0.014	—
17 Upper Quinault River	1982	53	0.904	0.096	—	—	—	—	—	—	—	—
15 Quinault NFH	[2]pre-1982	99	0.920	0.080	—	—	0.980	0.020	—	—	—	—
	1982	50	0.958	0.042	—	—	1.000	—	0.411	0.589	—	—
16 Quinault Pens	1982	50	0.870	0.054	0.076	—	1.000	—	0.500	0.500	—	—
Others												
18 Wynoochee River	1982	66	—	—	—	—	—	—	0.635	0.365	—	—
21 Elwha Spawning Channel	1981	39	—	—	—	—	—	—	0.500	0.500	—	—
	1982	40	0.962	0.038	—	—	1.000	—	0.237	0.745	—	—

[1]Offspring from these adults would have belonged to the 1983 year class.

[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Iddh-1,2*		*Idh-3,4*				*Mdh-1,2*		*Mdh-3,4*		
		100	36	100	120	87	60	100	120	100	115	67
Quillayute River												
1 Fall-run adults	[1](1983)	—	—	0.976	0.024	—	—	1.000	—	0.980	0.020	—
1 Summer-run adults	[1](1983)	—	—	0.928	0.072	—	—	1.000	—	0.971	0.025	0.004
3 Soleduck River	1981	—	—	0.911	0.057	0.032	—	0.987	0.013	0.993	0.007	—
	1982	—	—	1.000	—	—	—	1.000	—	0.975	0.025	—
4 Soleduck Hatchery												
Fall run	[2]pre-1982	—	—	0.990	0.010	—	—	1.000	—	0.990	0.010	—
	1982	—	—	1.000	—	—	—	1.000	—	0.938	0.062	—
Spring/summer run	[2]pre-1982	—	—	0.955	0.035	0.010	—	1.000	—	0.975	0.015	0.010
	1982	—	—	0.985	0.010	0.005	—	1.000	—	0.985	0.015	—
	[1](1983)	—	—	0.915	0.078	0.003	0.004	1.000	—	0.987	0.006	0.007
6 Bogachiel River	1981	—	—	0.946	0.054	—	—	1.000	—	0.975	0.025	—
	1982	—	—	1.000	—	—	—	1.000	—	0.888	0.112	—
Hoh River												
7 Fall-run adults	[1](1983)	—	—	0.910	0.090	—	—	1.000	—	0.959	0.041	—
7 Summer-run adults	[1](1983)	—	—	0.922	0.078	—	—	1.000	—	0.973	0.027	—
8 Juveniles	1981	—	—	0.929	0.071	—	—	1.000	—	0.996	0.004	—
	1982	—	—	0.996	0.004	—	—	1.000	—	0.990	0.010	—
Queets River												
9 Fall-run adults	[1](1983)	—	—	0.915	0.085	—	—	1.000	—	0.979	0.021	—
9 Summer-run adults	[1](1983)	—	—	0.928	0.072	—	—	1.000	—	0.992	0.008	—
10 Clearwater River	1981	—	—	0.903	0.060	0.037	—	1.000	—	0.961	0.039	—
	1982	0.897	0.103	0.825	0.175	—	—	1.000	—	0.970	0.025	0.005
12 Salmon River	1982	—	—	0.938	0.062	—	—	0.990	0.010	0.974	0.026	—
11 Upper Queets River	1981	—	—	0.873	0.127	—	—	1.000	—	0.996	0.004	—
	1982	—	—	0.936	0.064	—	—	1.000	—	0.995	0.005	—
Quinault River												
13 Adults	[1](1983)	—	—	0.952	0.048	—	—	1.000	—	0.988	—	0.012
14 Lower Quinault River	1982	—	—	0.943	0.057	—	—	1.000	—	0.991	0.009	—
17 Upper Quinault River	1982	—	—	0.931	0.069	—	—	1.000	—	0.990	0.010	—
15 Quinault NFH	[2]pre-1982	—	—	0.900	0.090	0.010	—	1.000	—	0.990	0.010	—
	1982	—	—	0.974	0.026	—	—	1.000	—	1.000	—	—
16 Quinault Pens	1982	—	—	0.978	0.022	—	—	1.000	—	0.995	0.005	—
Others												
18 Wynoochee River	1982	—	—	0.980	0.020	—	—	1.000	—	0.996	0.004	—
21 Elwha Spawning Channel	1981	—	—	0.894	0.106	—	—	1.000	—	0.929	—	0.071
	1982	0.938	0.062	0.950	0.050	—	—	1.000	—	1.000	—	—

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Mpi-1*			*Pgm-1*			*Pgdh-1*		*Pgk-2*	
		100	116	90	100	129	150	100	90	100	81
Quillayute River											
1 Fall-run adults	[1](1983)	0.672	0.328	—	0.909	0.091	—	1.000	—	0.512	0.488
1 Summer-run adults	[1](1983)	0.688	0.312	—	0.951	0.049	—	1.000	—	0.475	0.525
3 Soleduck River	1981	0.743	0.257	—	0.936	0.064	—	1.000	—	0.486	0.514
	1982	0.650	0.350	—	0.962	0.038	—	1.000	—	0.325	0.675
4 Soleduck Hatchery											
Fall run	[2]pre-1982	0.810	0.190	—	1.000	—	—	1.000	—	0.370	0.630
	1982	0.862	0.138	—	0.988	0.012	—	1.000	—	—	—
Spring/summer run	[2]pre-1982	0.620	0.370	0.010	1.000	—	—	1.000	—	0.490	0.510
	1982	0.580	0.410	0.010	0.990	0.010	—	1.000	—	0.610	0.390
	[1](1983)	0.753	0.247	—	0.980	0.020	—	1.000	—	0.617	0.383
6 Bogachiel River	1981	0.621	0.379	—	0.949	0.022	0.029	1.000	—	0.543	0.457
	1982	0.663	0.337	—	0.925	0.075	—	1.000	—	0.487	0.513
Hoh River											
7 Fall-run adults	[1](1983)	0.743	0.257	—	0.946	0.054	—	1.000	—	0.405	0.595
7 Summer-run adults	[1](1983)	0.738	0.262	—	0.886	0.114	—	1.000	—	0.473	0.527
8 Juveniles	1981	0.593	0.407	—	0.900	0.086	0.014	1.000	—	0.470	0.530
	1982	0.669	0.331	—	0.954	0.039	0.007	1.000	—	0.454	0.546
Queets River											
9 Fall-run adults	[1](1983)	0.704	0.296	—	0.914	0.086	—	1.000	—	0.467	0.533
9 Summer-run adults	[1](1983)	0.661	0.339	—	0.882	0.118	—	1.000	—	0.591	0.409
10 Clearwater River	1981	0.732	0.268	—	0.943	0.050	0.007	1.000	—	0.421	0.579
	1982	0.775	0.225	—	0.843	0.147	0.010	1.000	—	0.438	0.562
12 Salmon River	1982	0.638	0.362	—	0.906	0.052	0.042	1.000	—	0.562	0.438
11 Upper Queets River	1981	0.636	0.364	—	0.864	0.079	0.057	1.000	—	0.369	0.631
	1982	0.750	0.250	—	0.991	0.009	—	1.000	—	0.463	0.537
Quinault River											
13 Adults	[1](1983)	0.746	0.254	—	0.984	0.016	—	0.992	0.008	0.597	0.403
14 Lower Quinault River	1982	0.632	0.368	—	0.864	0.136	—	1.000	—	0.539	0.461
17 Upper Quinault River	1982	0.654	0.346	—	0.896	0.104	—	1.000	—	0.500	0.500
15 Quinault NFH	[2]pre-1982	0.610	0.390	—	0.930	0.050	0.020	—	—	0.580	0.420
	1982	0.786	0.214	—	0.970	0.030	—	0.980	0.020	0.776	0.224
16 Quinault Pens	1982	0.730	0.270	—	0.940	0.040	0.020	1.000	—	0.235	0.765
Others											
18 Wynoochee River	1982	0.723	0.269	0.008	0.917	0.083	—	1.000	—	0.632	0.368
21 Elwha Spawning Channel	1981	0.500	0.482	0.018	0.987	—	0.013	1.000	—	0.468	0.532
	1982	0.632	0.368	—	1.000	—	—	1.000	—	0.250	0.750

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Sod-1* −100	−225	400
Quillayute River				
1 Fall-run adults	[1](1983)	0.904	0.096	—
1 Summer-run adults	[1](1983)	0.860	0.140	—
3 Soleduck River	1981	0.903	0.097	—
	1982	0.975	0.025	—
4 Soleduck Hatchery				
Fall run	[2]pre-1982	0.800	0.200	—
	1982	0.833	0.167	—
Spring/summer run	[2]pre-1982	0.620	0.380	—
	1982	0.840	0.160	—
	[1](1983)	0.724	0.276	—
6 Bogachiel River	1981	0.885	0.115	—
	1982	0.926	0.074	—
Hoh River				
7 Fall-run adults	[1](1983)	0.892	0.108	—
7 Summer-run adults	[1](1983)	0.879	0.121	—
8 Juveniles	1981	0.886	0.114	—
	1982	0.868	0.132	—
Queets River				
9 Fall-run adults	[1](1983)	0.919	0.081	—
9 Summer-run adults	[1](1983)	0.852	0.148	—
10 Clearwater River	1981	0.913	0.080	0.007
	1982	0.907	0.093	—
12 Salmon River	1982	0.927	0.073	—
11 Upper Queets River	1981	0.886	0.107	0.007
	1982	0.861	0.139	—
Quinault River				
13 Adults	[1](1983)	0.703	0.297	—
14 Lower Quinault River	1982	0.949	0.051	—
17 Upper Quinault River	1982	0.824	0.176	—
15 Quinault NFH	[2]pre-1982	0.780	0.210	0.010
	1982	0.720	0.200	0.080
16 Quinault Pens	1982	0.929	0.071	—
Others				
18 Wynoochee River	1982	0.821	0.179	—
21 Elwha Spawning Channel	1981	0.741	0.259	—
	1982	0.697	0.303	—

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 2.—Allele frequencies for coho salmon from Washington. Each allele is designated by its mobility (relative to the common allele) times 100. *N* is the number of fish scored for most loci; however, fewer fish may have been scored at some loci. Frequencies from fewer than *N*/2 fish are identified with an asterisk, and frequencies from fewer than 25 fish are not shown and were not used in our analyses. Numbers preceding sample name correspond to locations shown in Figure 1.

			bGala-2		*Ah-3*				*Ada-2*			*Aat-3,4*	
	Brood	*N*	100	128	100	91	115	130	100	110	91	100	87
Quillayute River													
2 Dickey River	1981	52	—	—	0.990	—	—	0.010	0.990	0.010	—	1.000	—
3 Soleduck River	1981	37	0.660	0.340	0.973	0.027	—	—	0.933	0.967	—	1.000	—
	1982	48	0.583	0.417	1.000	—	—	—	1.000	—	—	1.000	—
4 Soleduck Hatchery	1981	40	—	—	0.988	0.012	—	—	1.000	—	—	1.000	—
5 Calawah River	1982	40	0.551	0.449	0.925	0.050	0.025	—	0.988	0.013	—	1.000	—
6 Bogachiel River	1982	74	0.546	0.454	1.000	—	—	—	1.000	—	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	48	0.061	0.399	1.000	—	—	—	0.990	0.010	—	1.000	—
Pin Creeks	1982	44	—	—	0.989	0.011	—	—	1.000	—	—	1.000	—
8 Other tributaries	1982	45	0.616	0.384	1.000	—	—	—	1.000	—	—	1.000	—
Queets River													
10 Clearwater River	1981	210	0.637*	0.363	0.979	0.021	—	—	0.995	0.005	—	1.000	—
11 Upper Queets River	1981	76	0.674	0.326	1.000	—	—	—	0.993	0.007	—	1.000	—
Quinalt River													
13 Lower Quinault River	1982	60	—	—	—	—	—	—	1.000	—	—	0.923	0.077
15 Quinault NFH	1981	40	—	—	1.000	—	—	—	0.961	0.039	—	1.000	—
	1982	40	0.814	0.186	0.988	0.012	—	—	0.988	—	0.012	1.000	—
Others													
19 Snohomish River	1981, 1982	106	0.595	0.405	0.986	0.009	0.005	—	1.000	—	—	1.000	—
20 Snow Creek	1981	60	0.542	0.458	1.000	—	—	—	—	—	—	1.000	—

		Ck-1		*Gpi-1*		*Gpi-2*			*Gpi-3*		*G3pdh-1*	
	Brood	100	127	100	250	100	157	67	100	90	−100	−15
Quillayute River												
2 Dickey River	1981	1.000	—	1.000	—	0.990	0.010	—	1.000	—	0.990	0.010
3 Soleduck River	1981	1.000	—	1.000	—	0.986	0.014	—	1.000	—	1.000	—
	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
4 Soleduck Hatchery	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.969	0.031
5 Calawah River	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	0.987	0.013
6 Bogachiel River	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
Hoh River												
8 Winfield, Nolan,	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
Pin Creeks	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	1.000	—	0.989	0.011	—	1.000	—	1.000	—
Queets River												
10 Clearwater River	1981	1.000	—	0.998	0.002	0.993	0.007	—	1.000	—	1.000	—
11 Upper Queets River	1981	1.000	—	0.993	0.007	0.993	—	0.007	1.000	—	0.987	0.013
Quinalt River												
13 Lower Quinault River	1982	1.000	—	1.000	—	0.991	0.009	—	1.000	—	—	—
15 Quinault NFH	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.959	0.041
	1982	1.000	—	1.000	—	0.950	0.050	—	0.975	0.025	1.000	—
Others												
19 Snohomish River	1981, 1982	0.995	0.005	1.000	—	0.981	—	0.019	1.000	—	1.000	—
20 Snow Creek	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.992	0.008

APPENDIX TABLE 2.—*Continued.*

	Brood	*Idh-3,4*					*Ldh-3*			*Ldh-4*		*Lgl-1*	
		100	130	70	123	157	100	45	140	100	110	100	80
Quillayute River													
2 Dickey River	1981	0.825	0.169	0.006	—	—	0.971	0.029	—	1.000	—	1.000	—
3 Soleduck River	1981	0.973	—	0.007	0.020	—	0.986	—	0.014	1.000	—	1.000	—
	1982	—	—	—	—	—	1.000	—	—	1.000	—	1.000	—
4 Soleduck Hatchery	1981	0.964	0.036	—	—	—	1.000	—	—	1.000	—	1.000	—
5 Calawah River	1982	1.000	—	—	—	—	1.000	—	—	1.000	—	0.963	0.037
6 Bogachiel River	1982	0.996	—	0.004	—	—	0.993	—	0.007	1.000	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	0.995	—	0.005	—	—	1.000	—	—	1.000	—	1.000	—
Pin Creeks	1982	0.978	—	0.022	—	—	0.988	0.012	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	—	—	—	0.989	0.011	—	1.000	—	1.000	—
Queets River													
10 Clearwater River	1981	0.924	0.073	0.001	0.002	—	0.993	0.007	—	1.000	—	1.000	—
11 Upper Queets River	1981	0.858*	0.132*	—	0.006*	0.004*	1.000	—	—	0.994	0.006	1.000	—
Quinalt River													
13 Lower Quinault River	1982	0.905	0.095	—	—	—	1.000	—	—	1.000	—	1.000	—
15 Quinault NFH	1981	0.917	0.077	—	—	0.006	1.000	—	—	1.000	—	1.000	—
	1982	1.000	—	—	—	—	0.988	0.012	—	0.975	0.025	1.000	—
Others													
19 Snohomish River	1981, 1982	0.920	0.070	0.007	—	0.003	1.000	—	—	0.972	0.028	1.000	—
20 Snow Creek	1981	0.985	0.015	—	—	—	1.000	—	—	1.000	—	1.000	—

	Brood	*Mdh-1,2*			*Mdh-3,4*					*Mdh-5*		*MdhP-1*	
		100	37	210	100	123	110	89	140	100	107	100	130
Quillayute River													
2 Dickey River	1981	1.000	—	—	0.991	0.009	—	—	—	0.971	0.029	1.000	—
3 Soleduck River	1981	1.000	—	—	0.967	0.020	—	—	0.013	—	—	1.000	—
	1982	1.000	—	—	1.000	—	—	—	—	—	—	—	—
4 Soleduck Hatchery	1981	1.000	—	—	1.000	—	—	—	—	—	—	1.000	—
5 Calawah River	1982	1.000	—	—	0.988	0.012	—	—	—	1.000	—	1.000	—
6 Bogachiel River	1982	1.000	—	—	0.993	0.007	—	—	—	—	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	1.000	—	—	0.985	0.005	0.010	—	—	1.000	—	1.000	—
Pin Creeks	1982	1.000	—	—	0.955	0.040	—	0.006	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	—	0.956	0.044	—	—	—	—	—	1.000	—
Queets River													
10 Clearwater River	1981	1.000	—	—	0.985	0.010	—	0.005	—	0.960	0.040	0.990	0.010
11 Upper Queets River	1981	0.994	0.003	0.003	0.997	0.003	—	—	—	1.000*	—	1.000	—
Quinalt River													
13 Lower Quinault River	1982	1.000	—	—	1.000	—	—	—	—	1.000	—	1.000	—
15 Quinault NFH	1981	1.000	—	—	1.000	—	—	—	—	0.950	0.050	1.000	—
	1982	1.000	—	—	0.994	0.006	—	—	—	—	—	1.000	—
Others													
19 Snohomish River	1981, 1982	0.997	0.003	—	0.998	0.002	—	—	—	1.000	—	1.000	—
20 Snow Creek	1981	1.000	—	—	1.000	—	—	—	—	—	—	1.000	—

APPENDIX TABLE 2.—*Continued.*

	Brood	*Mpi-1*		*Pgm-2*		*Pgdh-1*		*Pnp-1*	
		100	123	−100	−55	100	92	100	155
Quillayute River									
2 Dickey River	1981	1.000	—	0.990	0.010	1.000	—	—	—
3 Soleduck River	1981	1.000	—	1.000	—	1.000	—	—	—
	1982	1.000	—	1.000	—	1.000	—	—	—
4 Soleduck Hatchery	1981	1.000	—	1.000	—	1.000	—	—	—
5 Calawah River	1982	1.000	—	1.000	—	1.000	—	1.000	—
6 Bogachiel River	1982	1.000	—	1.000	—	1.000	—	—	—
Hoh River									
8 Winfield, Nolan,	1981	1.000	—	1.000	—	1.000	—	—	—
Pin Creeks	1982	1.000	—	1.000	—	1.000	—	0.673	0.327
8 Other tributaries	1982	1.000	—	1.000	—	1.000	—	—	—
Queets River									
10 Clearwater River	1981	0.995	0.005	1.000	—	1.000	—	0.877*	0.123*
11 Upper Queets River	1981	1.000	—	1.000	—	1.000	—	0.780*	0.220*
Quinault River									
13 Lower Quinault River	1982	1.000	—	1.000	—	0.974	0.026	—	—
15 Quinault NFH	1981	1.000	—	1.000	—	1.000	—	—	—
	1982	1.000	—	1.000	—	1.000	—	1.000	—
Others									
19 Snohomish River	1981, 1982	1.000	—	1.000	—	1.000	—	0.995	0.005
20 Snow Creek	1981	1.000	—	1.000	—	1.000	—	1.000	—

ASSESSMENT OF INTERACTION BETWEEN NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, FISHERIES BY USE OF A SIMULATION MODEL

P. KLEIBER AND B. BAKER[1]

ABSTRACT

Using a simulation model of a typical year in the North Pacific albacore fisheries in the 1970s, we tested for the degree to which the activity of fleets affects the performance of other fleets. The results show that rather drastic (factor of two) changes in the activity of any of the three principal albacore fleets have only a mild effect on the catch of the other fleets. With the overall exploitation rate in the model close to the exploitation rate determined from tagging results (6%), the maximum degree of interaction was a 7.5% drop in longline catch resulting from doubling the baitboat effort. The mild degree of interaction was insensitive to exploitation rate up to approximately 10% exploitation, although interaction became more severe at higher levels of exploitation.

Fishery interaction, the effect of one fishing fleet on another, is a phenomenon of growing concern to those involved in the management and development of pelagic fisheries. This concern has arisen from the growing awareness that oceanic fishery resources are not unlimited and from the evolution of exclusive economic zones to protect local interests against large international fishing fleets. Assessing the potential for interaction between tuna fisheries in different island countries was one of the principal reasons that the South Pacific Commission conducted the Skipjack Survey and Assessment Programme (Kearney 1983). Workshops on this topic have been held during international tuna fishery meetings, and a Tuna Fisheries Interaction Programme has been proposed within the Indo-Pacific Tuna Development and Management Programme.

Because there is a multiplicity of fleets and nations involved in harvesting albacore, *Thunnus alalunga*, a tuna, in the North Pacific, there is a potential concern about interaction between these fleets. A history of North Pacific albacore fishing since the 1950s is summarized by Laurs (1983). Three principal fleets have been responsible for the catch: the Japanese baitboat, the Japanese longline, and the United States jigboat fleets (Fig. 1). In the 1970s these accounted for more than 90% (60%, 15%, and 18%, respectively) of the total catch. In recent years, Japanese gill net gear has become important, accounting for approximately 20% of the total catch from 1981 through 1983 (Fig. 1). Detailed statistics on this emerging fishery are not currently available.

Among the three principal fleets, the U.S. fleet tends to take the smallest fish, and the longline the largest, but the size distributions in the catch overlap to a large extent (Fig. 2). The geographic distribution of the fleets is indicated in Figure 3, but the overlap is overemphasized because there is seasonal separation in many cases. Nevertheless, the migratory nature of albacore makes for potentially significant interaction between fleets that are separated in time and space.

Because there have been no clear trends in catch or in catch per effort (Laurs 1983), it has been assumed that the albacore stocks have not been adversely affected by the fisheries, and such woes as the fishermen have had have not been blamed on poor status of stocks. Therefore there has been little reason for fleets to accuse one another of depleting the stocks and thus little concern about fishery interaction. To verify that sanguine view, we have estimated the degree of interaction between the three principal albacore fisheries in the North Pacific. We defined interaction to be the degree to which changes in the activity (effort) of one fleet affect the performance (catch) of another fleet. The magnitude of this kind of interaction cannot be calculated directly from fishery data, nor can controlled, real-life experiments be conducted on the grand scale necessary to address this topic. However, experiments conducted on simulation model are feasible. The results of such experiments with an

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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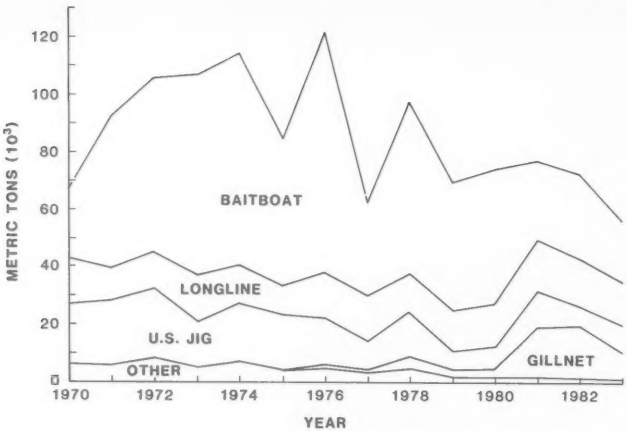

FIGURE 1.—Annual catch of albacore by gear type. [Data from Majors and Miller. 1985. Summary of the 1984 North Pacific albacore fishery data. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-85-14, 45 p.]

albacore simulation model are the subject of this report.

THE MODEL

We used a model that incorporates recruitment, growth, migration, natural mortality, and harvest of albacore by the Japanese baitboat fleet, the Japanese longline fleet, and the United States surface fleet (primarily jig gear). Our approach was to manipulate the effort of one fleet at a time and note the effect on the catch of the other fleets.

A full technical description of the model is given by Kleiber and Baker[2]. We discretized fish size into 5 cm length classes and the North Pacific range of albacore into nine geographic zones (Fig. 3). The basic dynamics within a size class and zone are described by the following differential equation:

$$\frac{dP_{s,z}(t)}{dt} = G_{s-1}P_{s-1,z}(t) + \sum_{\bar{z}} \mu_{\bar{z}\to z}\, P_{s,\bar{z}}(t)$$

$$- \left[M + G_s + \sum_{\bar{z}} \mu_{z\to\bar{z}}\right] P_{s,z}(t) - \sum_{g} c_{s,z,g}$$

where $c_{s,z,g} = q_{s,g}\, f_{z,g}(t)\, P_{s,z}(t)$ is the catch rate (number per unit time) by size, zone, and gear. The symbols are defined as follows:

s —index for size class
z —index for geographic zone
$\bar{z}$ —index for zone adjacent to z
g —index for gear type
$P_{s,z}(t)$ —population (numbers) by size and zone at time t

the following being input parameters:

$P_{0,z}(t)$ —recruitment rate by zone at time t
G_s —proportion growing out of size s per unit time
G_0 —always = 1 (so that $P_{0,z}(t)$ is recruitment rate)
$\mu_{z_1\to z_2}$ —coefficient of migration from zone z_1 to zone z_2
M —natural mortality
$q_{s,g}$ —catchability by size and gear
$f_{z,g}(t)$ —effort by zone and gear at time t.

INPUT PARAMETER VALUES

Full details of how input parameters were estimated are given by Kleiber and Baker (fn. 2). The following is a summary.

The most complete catch and effort data sets that were available to us and that cover the three

[2]Kleiber, P., and B. Baker. 1987. The North Pacific albacore simulation model. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-87-2, 38 p.

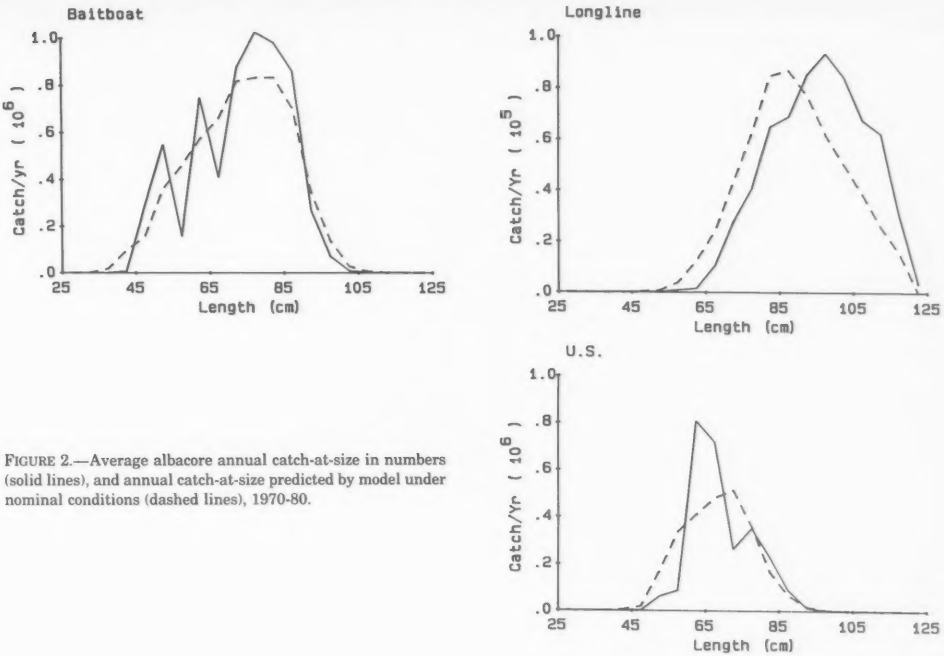

FIGURE 2.—Average albacore annual catch-at-size in numbers (solid lines), and annual catch-at-size predicted by model under nominal conditions (dashed lines), 1970-80.

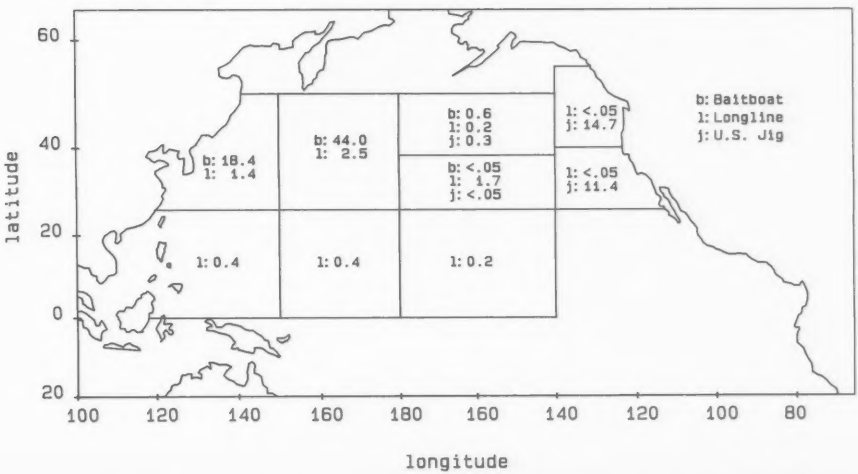

FIGURE 3.—Model zones with average annual albacore catch (numbers × 10^5) by gear type, 1970-80.

major fleets span the years 1970 through 1980. We processed the data into an "average year", that is, the average (over the years 1970-80) of catch by size, zone, month, and gear and the average of effort by zone, month, and gear (Kleiber and Baker[3]). The effort values were used directly in the model and the catch and effort used to estimate other input parameters.

We estimated the 1970-80 average recruitment and preliminary catchability values by size and gear by use of a size-structured cohort analysis (Jones 1981). The catch-at-size vector necessary for this cohort analysis was obtained from the average year by aggregating over zones, averaging over months, and smoothing over size classes.

To conduct the cohort analysis, we needed to specify an average final cohort size, which was unknown to us. We tried a series of values and chose results for which the overall exploitation rate (catch divided by recruitment estimate) was close to the overall exploitation rate estimated from tagging. Tagged albacore have been released in the U.S. fishery at an average size of approximately 65 cm, and approximately 6% of the tags have been recovered (Laurs[4]). Nonreporting losses are small for the major fisheries that recovered the tags (Laurs[5]). Assuming a value of 10% for nonreporting and Type I and II tag losses of 12% and 0.098 $year^{-1}$ respectively (Laurs et al. 1976), the exploitation rate of recruits to 65 cm should be approximately twice the raw recovery percentage. But the exploitation rate in the cohort analysis and the simulation model is based on recruits to 25 cm which should be approximately twice as numerous as recruits to 65 cm (based on growth and natural mortality rates used in the model). Therefore, the exploitation rate of recruits to 25 cm should be approximately equal to the raw tag recovery percentage (6%). We chose a cohort analysis with an exploitation rate of 6.3% as the basis for the results presented below except where we discuss sensitivity to exploitation rate for which we repeated the analysis several times starting at this point with a series of cohort analyses at a series of higher exploitation rates.

[3]Kleiber, P., and B. Baker. 1986. Development of catch and effort data base for the North Pacific albacore simulation model. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-86-26, 21 p.

[4]Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-79-17, 10 p.

[5]R. M. Laurs, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1987.

The cohort analysis yielded a Pacific-wide recruitment estimate. We apportioned one third of this recruitment to each of the three southern zones, where albacore larvae are predominantly found (Nishikawa et al. 1984).

Size-specific overall fishing mortalities obtained from the cohort analysis were apportioned to gear type by the proportion of the total catch at each size that is taken by each gear type in the average year. We then converted the fishing mortalities into catchabilities by dividing by the overall average effort for each gear type.

Size-specific growth coefficients, G_s, were the growth rates in length (dl/dt) at the upper end of each size class divided by the length of the size classes (5 cm). We estimated the growth rates from the derivative form of the von Bertalanffy growth equation

$$\frac{dl}{dt} = k(l_\infty - 1)$$

where l_∞ is 135.6 cm and k is 0.014 $month^{-1}$ (Clemens 1961). We used these same values in the size-structured cohort analysis, which required input of growth information.

A value for natural mortality was also needed both in the cohort analyses and in the model. We used a value of 0.017 $month^{-1}$ (0.2 $year^{-1}$) (Suda 1966).

The tag data would be a good source of information to estimate migration coefficients except that the tag recovery effort is not uniformly distributed and analytical techniques to deal with that situation are not well developed. To get a reasonable set of migration coefficients, we quantified the experience of three experts, scientists knowledgeable about the North Pacific albacore fisheries and the available tag data. We first asked the experts to identify the significant paths (movement from one zone to an adjacent zone) for each of a series of broad (10 cm) size classes. For each path we then asked how the intensity of migration via that path is distributed over the months of the year and we evaluated the average intensity by asking the experts the following question: On average, during the season of this migration, if 100 fish of the given size class are now in the origin zone, how many of these (irrespective of mortality) would be expected to be in the destination zone one month from now? We calculated the average migration coefficient for the particular path by

$$\bar{\mu} = \ln\left[\frac{100}{100 - X}\right]$$

where X is the answer to the above question. The monthly migration coefficients were then obtained by scaling the distribution of intensity over months so that the average was equal to $\bar{\mu}$. The migration coefficients for the 10 cm size classes were then assigned to the smaller (5 cm) size classes used in the model, and the coefficients smoothed over size to soften discontinuities.

The pattern of movement represented by the migration coefficients can be summarized as follows: For immature fish (<85 cm) in the zones north of 25° north the pattern is vigorous seasonal movement toward the east in the summer and toward the west at other times. New recruits, which appear in the southern zones, migrate mainly northward throughout the year and are entrained in the east-west excursions of the northern zones. Mature fish (>85 cm) accumulate in the southern zones with brief movements northward in April and May.

RESULTS

When we ran the model with input values estimated as described above and with the effort of all fleets set at nominal levels, that is, the average seasonal and geographic pattern and magnitude of effort for the 1970s with the pattern repeated year after year, we found that after 10 years of simulation the seasonal and geographic pattern and magnitude of catch closely repeated itself year after year. Therefore in making comparisons of model results under different conditions, we allowed the model to run at least 10 years under a given repetitive annual regime before recording the catch results during 1 year of simulation.

In using the preliminary catchability values in the model, we found that the predicted catches were too low and the exploitation rate achieved (2.6%) was less than half the exploitation rate in the cohort analysis, which estimated those catchability values (6.3%). This is because the cohort analysis could not deal with geographic and seasonal variability. The fleets were presumed to be harvesting the ocean-wide population rather than the fish in a localized area and time as in the simulation model. We therefore scaled the catchabilities of each fleet upward to make the annual catches in number in the model (after 10 years of simulation) close to the real average annual catches (Kleiber and Baker fn. 2). With the corrected catchabilities, an exploitation rate of 5.1% was achieved and we took the results in this case to be our nominal (control) results (Fig. 2, Table 1).

We then made runs in which the original seasonal and geographic pattern of effort was maintained but the magnitude of effort of one of the fleets was either doubled or halved. We could then compare the annual catch of each fleet under the changed (experimental) conditions with the annual catch under nominal conditions.

TABLE 1.—Average albacore annual (1970-80) catch in numbers and metric kilotons (kt) by baitboat, longline, and U.S. fleets plus annual catch from model after at least 10 years of simulation under nominal conditions and under various conditions of altered fishing effort.

		baitboat		longline		U.S.	
		number (10^6)	kt	number (10^6)	kt	number (10^6)	kt
average catch		6.29	57.52	0.68	13.30	2.65	19.56
nominal effort		6.87	55.12	0.66	9.47	2.67	18.32
baitboat effort	× 2	12.89	102.00	0.62	8.76	2.63	18.05
	÷ 2	3.55	28.69	0.69	9.86	2.69	18.46
longline effort	× 2	6.85	54.91	1.32	18.79	2.67	18.30
	÷ 2	6.88	55.23	0.33	4.75	2.67	18.33
U.S. effort	× 2	6.80	54.43	0.65	9.23	5.19	35.41
	÷ 2	6.90	55.49	0.67	9.59	1.35	9.32

The catch-at-size for the three fleets under nominal and experimental conditions is plotted in Figures 4 to 6. Changes in effort in one fleet appear to have little effect on the size distribution in the catch of any of the fleets.

The effect on amount caught is another matter. Total catch of all sizes, both in numbers and in weight, is given in Table 1. We obtained catch in weight by converting the number caught in each length category to weight using the length-weight relationship of Clemens (1961) and then by summing over length categories. The effects are summarized in Tables 2 and 3 where the change from nominal catch for each fleet is given for each experimental treatment. By far the largest effect of a change in effort of any fleet is the effect on its own catch. A doubling of the baitboat effort causes the largest between-fleet effect, which is a 7.5% depression of the longline catch in weight, a loss of approximately 700 t (Table 3). A similar loss to the baitboat fleet, due to doubling of U.S. effort, is only a 1.3% decrease in the baitboat catch (Table 3).

We tested the sensitivity of our results to the

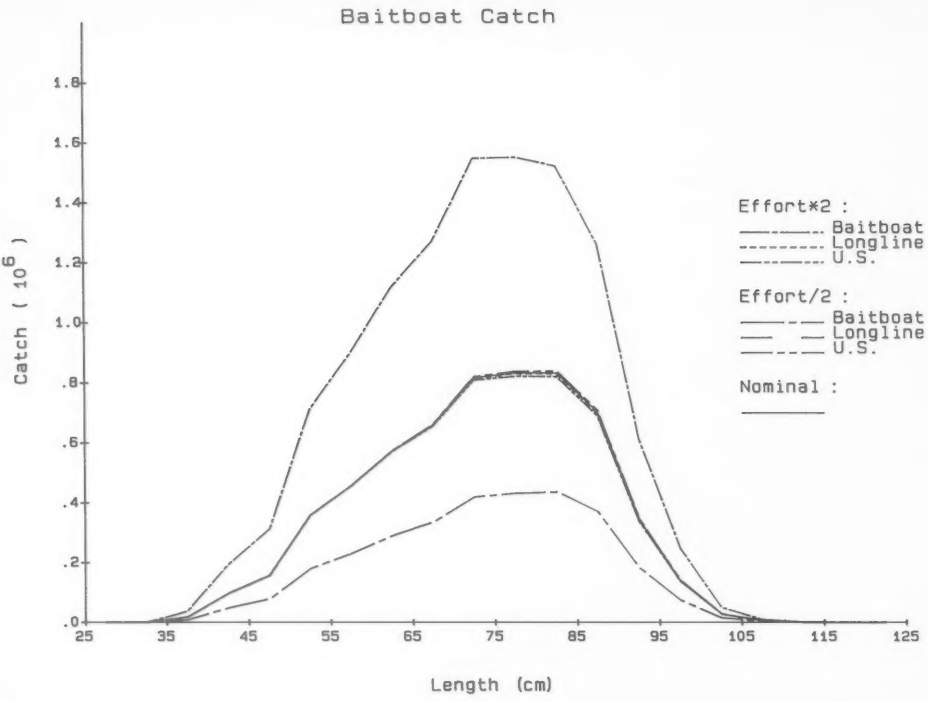

FIGURE 4.—Annual albacore baitboat catch-at-size in numbers predicted by the model under nominal and experimental conditions.

TABLE 2.—Interaction matrix for annual albacore catch in numbers. The values given are the differences between the catch under altered effort and the nominal catch (percent of nominal catch in parentheses).

cause ⇓	effect ⇒	Δ catch: number × 10^6 (%)		
		baitboat	longline	U.S.
baitboat	× 2	6.02 (87.6)	−0.04 (6.1)	−0.04 (1.5)
effort	÷ 2	−3.32 (48.3)	0.03 (4.5)	0.02 (0.7)
longline	× 2	−0.02 (0.3)	0.66 (100.0)	0.00 (0.0)
effort	÷ 2	0.01 (0.1)	−0.33 (50.0)	0.00 (0.0)
U.S.	× 2	−0.07 (1.0)	−0.01 (1.5)	2.52 (94.4)
effort	÷ 2	0.03 (0.4)	0.01 (1.5)	−1.32 (49.4)

TABLE 3.—Interaction matrix for annual albacore catch in weight. The values given are the differences between the catch under altered effort and the nominal catch (percent of nominal catch in parentheses).

cause ⇓	effect ⇒	Δ catch: kt (%)		
		baitboat	longline	U.S.
baitboat	× 2	46.88 (85.1)	−0.71 (7.5)	−0.27 (1.5)
effort	÷ 2	−26.43 (47.9)	0.39 (4.1)	0.14 (0.8)
longline	× 2	−0.21 (0.4)	9.32 (98.4)	−0.02 (0.1)
effort	÷ 2	0.11 (0.2)	−4.72 (49.8)	0.01 (0.1)
U.S.	× 2	−0.69 (1.3)	−0.24 (2.5)	17.09 (93.3)
effort	÷ 2	0.37 (0.7)	0.12 (1.3)	−9.00 (49.1)

overall exploitation rate by repeating the whole analysis at higher exploitation rates, starting with the cohort analysis, correcting catchabilities to give a new set of nominal results, and finally measuring the most sensitive interaction, the effect of doubled baitboat effort on the longline catch (Fig. 7). The degree of interaction is not affected very much when the exploitation rate is below 10%, but it rises quickly at higher exploitation rates.

DISCUSSION

Our results support the notion that fishery interaction is not of great consequence, at least for the North Pacific albacore fisheries typical of the

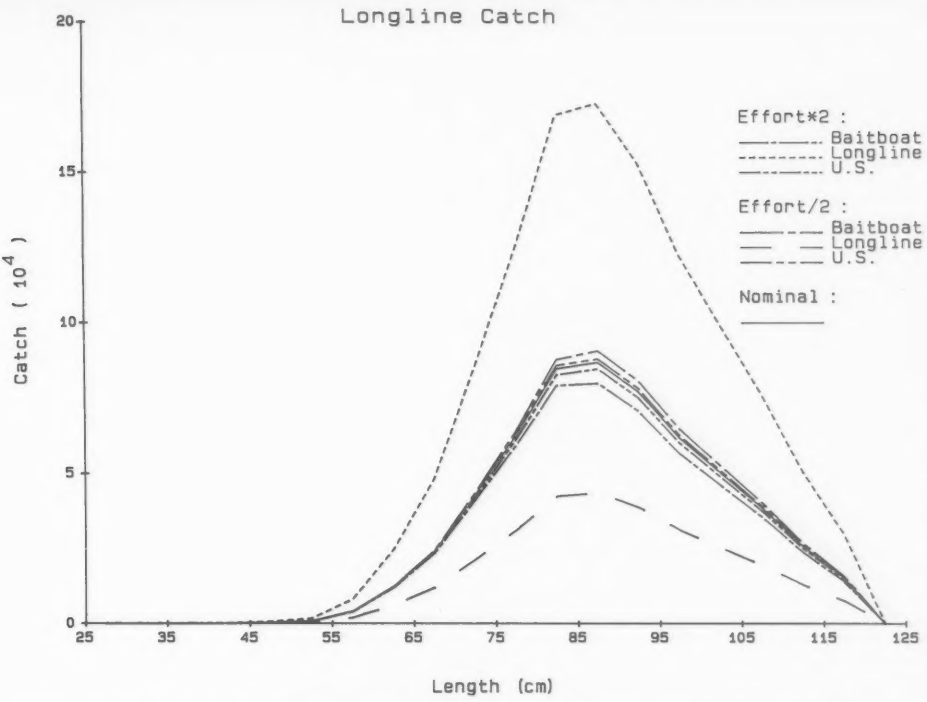

FIGURE 5.—Annual albacore longline catch-at-size in numbers predicted by the model under nominal and experimental conditions.

1970s. The reliability of this conclusion, of course, depends on the reliability of our simulation model, but in evaluating the behavior of the model, we should remember that what is important is the response of the model to experimental manipulation not the exactitude of the nominal behavior in comparison to real data. Of course, if the nominal behavior is outlandish, the responses to manipulation will be suspect. Therefore we used the average year as a signpost to tune the nominal results of the model into the range of plausible behavior, but we did not insist on exact duplication of the average year (itself an abstraction that never happened in reality).

A case in point is the longline catch, which under nominal conditions in the model is less (in weight) than any of the real annual longline catches for the years 1970-80. The average over those years is 13.3 metric kilotons (kt) per year whereas the nominal longline catch in the model is 9.47 kt/year (Table 1). The discrepancy is explained by the fact that the average size of fish in the model longline catch is less than the average size in the real longline catch, because large fish in the model migrate out of reach of the longline fleet more than they should. We have not corrected this problem because we are waiting for further information from tagging studies to get better estimates of migration coefficients. We expect the corrections to be quantitative refinements of the existing values and not a qualitative change in the current migration pattern in the model.

What is important in the current context is that bias in the nominal results is bound to show up in the experimental results as well. The migration coefficients were the same in both control and experimental situations in the model. Therefore, refinements to the coefficients are not likely to make much difference in the relative values in Tables 2 and 3, particularly in the percentages. It is pertinent that our conclusion of low interaction

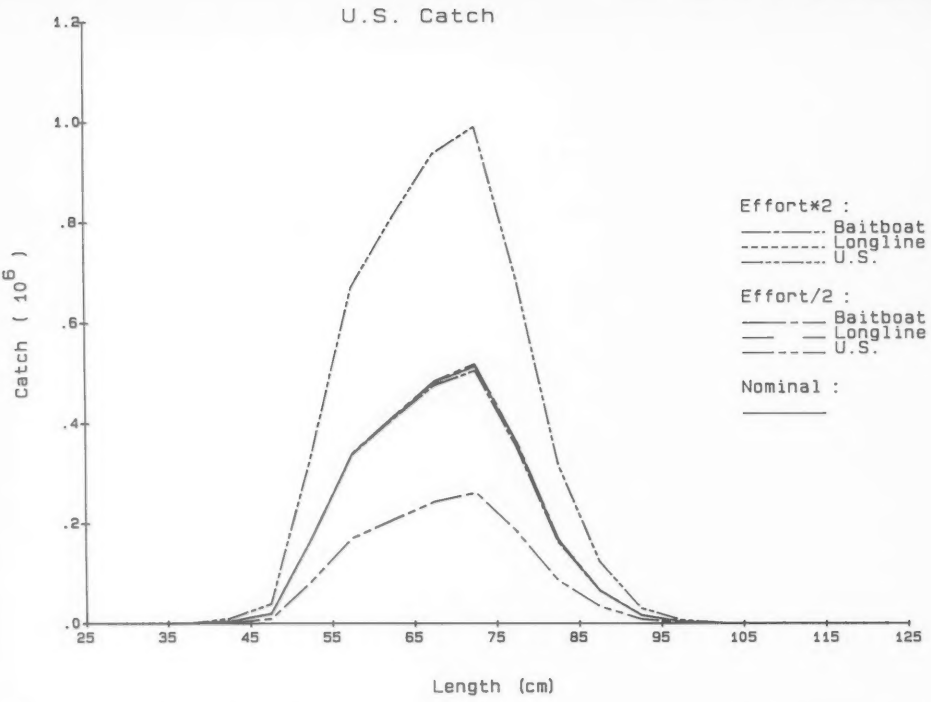

FIGURE 6.—Annual albacore U.S. catch-at-size in numbers predicted by the model under nominal and experimental conditions.

(expressed as percent) persisted through a series of updates of the model (such as changes in configuration of geographic strata) and inevitable updates and corrections of the fishery data base.

Though the nominal behavior of the model need not conform precisely to the mean behavior of albacore fisheries in the 1970s (however that might be defined), the behavior should, nonetheless, be a plausible representation of the albacore fisheries in that period. We have seen, for example, that our conclusion would be suspect if the actual exploitation rate were considerably higher than the 6% value that we assumed (Fig. 7), but such high exploitation levels would be contrary to the tag return results.

We have only tested the effects of changes in the magnitude of effort, not changes in seasonal and geographic pattern of effort, which might cause the fleets to overlap much more than they do. However, our experimental treatment of doubling the effort of a fleet is tantamount to adding

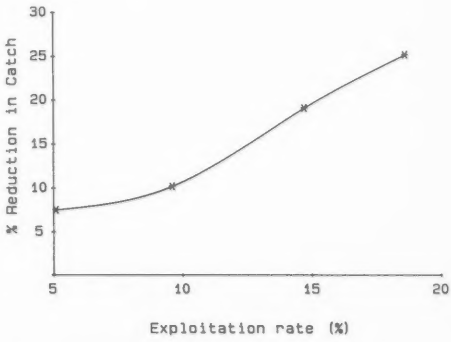

FIGURE 7.—Sensitivity of interaction to overall exploitation rate. The ordinate is the percent reduction from nominal levels in annual albacore longline catch in weight as a result of doubling the baitboat effort.

a completely overlapping, competing fleet. The response of each fleet to doubling of its own effort was close to a 100% increase in catch (Tables 2, 3), indicating that the degree of competition was low. Therefore, it would be difficult to design a realistic experimental treatment that 1) would be simply a shift in the geographic and seasonal pattern of effort in one fleet (not a change in magnitude), and 2) would have a strong impact on another fleet.

A legitimate question is whether our conclusions, which are based on 1970s data, can be extrapolated to the current conditions. The most striking change in recent years is the emergence of the gill net fishery for albacore, which now takes approximately 20% of the total catch. However, because the total catch has not increased, the exploitation rate must still be mild, and we would expect that interaction between fleets would also still be mild. We cannot use our model to estimate interaction quantitatively in this situation because we lack detailed data on the gill net fishery.

CONCLUSIONS

The implication of our results is that fleet interaction is not likely to be significant if the pattern and magnitude of effort in the 1970s are maintained. This assessment could change if the overall exploitation rate increases considerably. The recent emergence of the gill net fishery could be of significance in this regard. The levels of annual catch that have been reported by this fishery are not likely to be of concern, but the significance cannot be confidently evaluated unless detailed catch, effort, and size distribution data are made available.

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AGE DETERMINATION OF PACIFIC COD, *GADUS MACROCEPHALUS*, USING FIVE AGEING METHODS[1]

HAN-LIN LAI,[2] DONALD R. GUNDERSON,[3] AND LOH LEE LOW[4]

ABSTRACT

A comparative study of age determination methods for Pacific cod, *Gadus macrocephalus*, was carried out using dorsal and pectoral fin rays, scales, otoliths, and coracoids. A preliminary validation using the modal length of a strong year class confirmed that sections of dorsal fin rays were the most reliable ageing method. A Monte Carlo method was developed for converting scale ages to dorsal fin-ray ages. An analysis by log-linear model was developed for testing the effects of ageing method and age class on repeatability of age reading.

Scales have been widely used for ageing Pacific cod, *Gadus macrocephalus*, in the North Pacific since Kennedy (1970) developed the method for fish in Hecate Strait, British Columbia. However, Bakkala (1981)[5] found that the scale method may not be an appropriate ageing method since the estimated ages from scales do not appropriately reflect the progress of known year classes in the eastern Bering Sea. Beamish et al. (1978) also found that Kennedy's criteria might not be satisfactory for scales from juvenile Pacific cod in Canadian waters.

Beamish (1981) reported that thin sections of fin rays can be reliably aged and might be more accurate than scale ages when ageing older fish. However, Westrheim and Shaw (1982) encountered difficulties with fin-ray cross sections and reported that fin-ray ages were younger than scale ages. They also discovered false checks on the scales during the first year of life, which fitted the annulus criteria of Kennedy (1970), and validated the scale ageing method for age-1 and -2 Pacific cod. Chilton and Beamish (1982) noted problems associated with scales and fin rays, and recommended a judicious mixture of scale ages, fin-ray ages and length-frequency analysis for ageing Pacific cod in Canadian waters.

In earlier studies, Mosher (1954), Moiseev (1953), and Ketchen (1970) reported that the otolith surface ageing method was not satisfactory for Pacific cod. Ketchen (1970) also had no success with ageing of vertebrae, or opercula. Lai (1985) reported that age determination from the bony tissues in the gillcover, scapula, and cleithrum was not feasible.

This paper reports the results of a comparative study and preliminary validation of age determination methods for Pacific cod in the eastern Bering Sea using dorsal and pectoral fin rays, scales, otoliths and coracoids. In addition, we develop a method to convert scale ages to dorsal fin-ray ages. This age conversion method makes it possible to use existing ages estimated from scales.

MATERIALS AND METHODS

Dorsal and pectoral fin rays, otoliths, and scales were taken from 230 Pacific cod collected from foreign fishing vessels operating in the eastern Bering Sea during September 1983 to March 1984. Among these samples, coracoids were also taken from 101 fish.

Dorsal and pectoral fin-ray sections were prepared using an Isomet low-speed saw (Lai 1985), and the annuli were identified by the criteria of Beamish (1981) and Chilton and Beamish (1982). Scale images were made by acetate plate (Koo 1962) and then read by a microfisch reader. Annuli on scales were identified by the methods de-

[1]Contribution No. 726, School of Fisheries, University of Washington, Seattle, WA.

[2]School of Fisheries, WH-10, University of Washington, Seattle, WA 98195; present address: Center for Quantitative Sciences, HR-20, University of Washington, Seattle, WA 98195.

[3]School of Fisheries, WH-10, University of Washington, Seattle, WA 98195.

[4]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115.

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scribed in Westrheim and Shaw (1982). Otoliths must be sectioned with a low-speed electric saw and burnt with care, as they are quite brittle. The interpretation of annuli on break-and-burn surfaces was adapted from that of walleye pollock (Lai and Yeh 1986).

The coracoid is a dermal bone connected to the scapula and radii in the pectoral girdle. A triangular component within the coracoid (Fig. 1) shows alternate opaque (dark) and translucent (light) zones under a binocular microscope and transmitted light, by which annuli can be identified. The center of this structure occasionally contains some checks that are parallel to the annulus; however, their spacing is narrower than that of regular annuli. The age samples were read

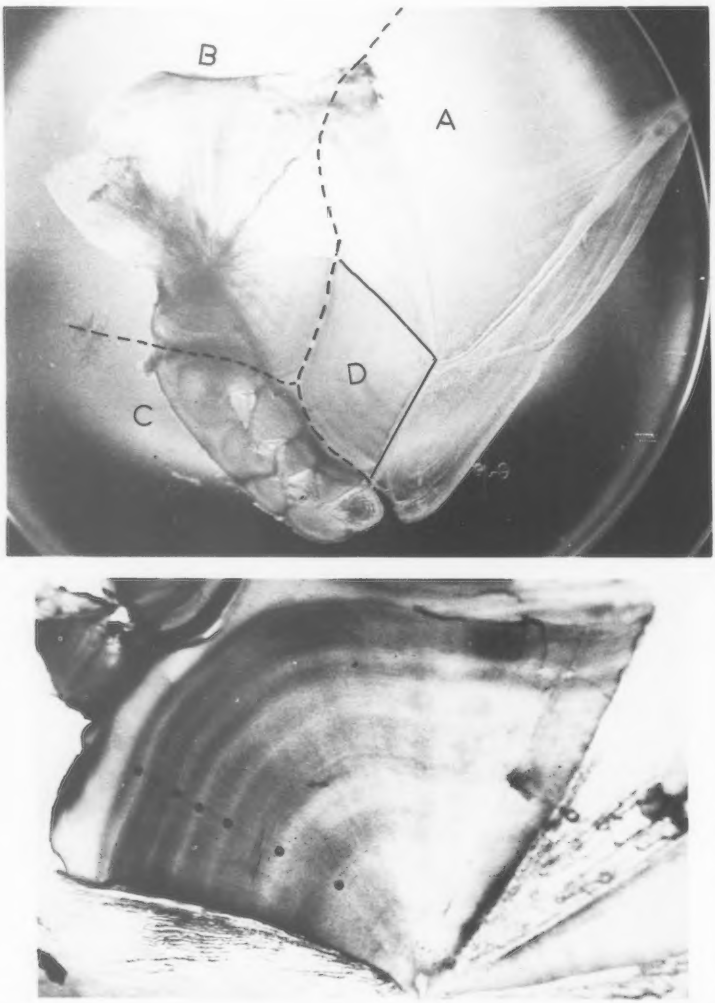

FIGURE 1.—Upper: The pectoral girdle. A, coracoid; B, scalpula; C, radii; D, the portion used for age determination. Lower: Enlarged Part D. •, translucent zone, counted as an annulus.

twice by the senior author, who had 3 years experience in age determination using all of the ageing methods.

A loglinear model (Fienberg 1981) was used to test the independence of repeatability ($R, k = 1, 2$ corresponding to agreement and disagreement) of age readings corresponding to age-class (A, $j = 1,...,8$ corresponding to age classes given in Table 1) and ageing method (M, $i = 1,...,5$ corresponding to ageing methods in the sequence given in Table 1). See Appendix A for the details of this statistical method. The computer program P4F in BMDP (Dixon 1983) was used for computation and analysis.

TABLE 1.—Observed frequency of agreement between two age readings using different ageing methods. Percent agreement is shown in parentheses.

Method (M)	Age (A)	Repeatability (R)		
		Agree	Disagree	Total
Coracoid	under 2	9 (100)	0	9
	3	1 (50)	1	2
	4	10 (77)	3	13
	5	12 (60)	8	20
	6	18 (67)	9	27
	7	5 (45)	6	11
	8	3 (43)	4	7
	over 9	4 (40)	6	10
Total		62 (63)	37	99
Break-and-burn	under 2	9 (90)	1	10
	3	7 (64)	4	11
	4	8 (73)	3	11
	5	41 (67)	20	61
	6	35 (58)	25	60
	7	14 (39)	22	36
	8	6 (35)	11	17
	over 9	9 (41)	13	22
Total		129 (57)	99	228
Dorsal fin ray	under 2	9 (100)	0	9
	3	2 (67)	1	3
	4	13 (81)	3	16
	5	36 (77)	11	47
	6	40 (82)	9	49
	7	24 (69)	11	35
	8	9 (39)	14	23
	over 9	7 (29)	17	24
Total		140 (68)	66	206
Pectoral fin ray	under 2	8 (100)	0	8
	3	6 (75)	2	8
	4	18 (64)	10	28
	5	36 (68)	17	53
	6	24 (45)	29	53
	7	12 (43)	16	28
	8	10 (45)	12	22
	over 9	3 (25)	9	12
Total		117 (55)	95	212
Scale	under 2	9 (82)	2	11
	3	11 (61)	7	18
	4	60 (74)	21	81
	5	48 (64)	27	75
	6	11 (38)	18	29
	7	1 (11)	8	9
	8	0 (0)	1	1
	over 9	0 (0)	1	1
Total		140 (62)	85	225

An analysis of variance (ANOVA) model with repeated measures (Winer 1971) was used to examine variability in age readings due to the methods. The ANOVA model was

$$X_{ijn} = \mu + \pi_n + M_i + (M\pi)_{in} + R_j + (R\pi)_{jn} + (MR\pi)_{ijn} + \epsilon_{ijn}$$

where, X_{ijn} is the observed age of the nth fish by the ith ageing method and jth reading,

$i = 1, 2, 3, 4, 5$ indicates ageing methods in the sequence shown in Table 1,

$j = 1, 2$ indicates the first and second age readings,

$n = 1,...,N$ indicates number of fish,

μ is the grand mean,

π is the effect between subjects (individual fish),

M is the effect of ageing method,

R is the effect of reading,

$(M\pi)$, $(R\pi)$, and $(MR\pi)$ are the two- and three-factor interactions of effects M, R, and π, and

ϵ is the random error.

Readings from coracoids were not included in the analysis because of the small sample size. Specimens with missing values were also excluded from this analysis. The Q-statistic (Snedecor and Cochran 1967) was used to test the differences between the mean ages between readings and between ageing methods.

Validation of age determination was carried out by comparing the mean lengths at age estimated from the five ageing methods to the modal lengths of the 1977 year class. The progression of this year class could be traced by examining the length-frequency distributions for 1978 to 1983.

Because existing age data files for Pacific cod at the Northwest and Alaska Fisheries Center (NWAFC) were derived from scales, it is important to explore whether or not the scale age data can be used for stock assessment. A simulation study was carried out to convert a scale age-length key to a dorsal fin-ray age-length key,

since the dorsal fin-ray method provides more accurate ages.

Age-length keys, derived from scales collected in 1979 and 1980 NWAFC demersal trawl surveys in the eastern Bering Sea, and length-frequency distributions obtained from these surveys were used as basic data to be converted. The classification probabilities for fin rays vs. scales were constructed from 966 age readings on dorsal fin rays and scales from the same fish collected in 1983-84 (Table 2). Each fish in the 1979 and 1980 scale age-length key was assigned a "pseudo" dorsal fin-ray age, which was a random variate generated from the subprogram GGDA in IMSL (International Mathematical and Statistical Library). The GGDA subroutine used the prior probability density in Table 2 corresponding to the scale age and length group to which the fish belongs. This was done 30 times to create 30 converted age-length keys each for 1979 and 1980. Then, mean lengths at age were determined from each converted age-length key, and age compositions were estimated by the method described in Lai (1987). These simulated results were compared with those from length-frequency analysis (Lai 1985).

RESULTS

Table 1 shows that the age readings from dorsal fin rays had the highest percent agreement (68%), followed by coracoids (63%), scales (62%), otoliths (57%), and pectoral fin rays (55%). Furthermore, the percent agreement for the major age classes in the fishery (ages 4-7) were much higher than for the other methods. To confirm this result, a log-linear model was fitted to the data in Table 1.

Table 3 shows that the best log-linear model (Appendix A) was

$$\theta_{ijk} = \log(m_{ijk}) = \mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA} \quad (2)$$

TABLE 2.—Observed classification probability for age readings from scales and dorsal fin-rays.

Scale age	Length (cm)	Dorsal fin-ray age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
1	20-29	1.0														20
1	30-39		1.0													6
2	30-39		1.0													8
2	40-49			0.750	0.250											8
3	30-39		1.0													2
3	40-49			0.333	0.667											3
3	50-59				0.188	0.375	0.375	0.063								32
3	60-69				0.087	0.565	0.174	0.130	0.043							23
4	40-49				0.133	0.467	0.400									15
4	50-59				0.604	0.264	0.094	0.038								53
4	60-69				0.066	0.377	0.221	0.197	0.098	0.041						122
4	70-79					0.153	0.350	0.190	0.065	0.058	0.066	0.051	0.036	0.029		137
4	80-89						0.348	0.217	0.174	0.130	0.043	0.087				23
5	50-59				0.143	0.857										14
5	60-69				0.043	0.391	0.239	0.196	0.109	0.022						92
5	70-79				0.005	0.095	0.264	0.206	0.180	0.116	0.069	0.048	0.016			189
5	80-89						0.154	0.128	0.205	0.256	0.154	0.077	0.026			39
5	90-99										0.500	0.500				2
6	60-69							0.611	0.222	0.167						18
6	70-79				0.017	0.083	0.333	0.233	0.167	0.117	0.033	0.017				60
6	80-89						0.188	0.344	0.156	0.125	0.125	0.063				32
6	90-99							0.059	0.412	0.176	0.118	0.118	0.118			17
6	100-109										0.500	0.500				4
7	70-79						0.333	0.111	0.333	0.111					0.111	9
7	80-89						0.182			0.545		0.182		0.090		11
7	90-99							0.063	0.187	0.250	0.187	0.063	0.250			16
8	80-89									0.400	0.200	0.400				5
8	90-99									0.333		0.167	0.333	0.167		6

TABLE 3.—Test for the independence of percent agreement (R) of age readings correlated to age-class (A) and ageing method (M).

Model	df	G^2	Probability
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA} + \lambda_{ijk}^{MAR}$	0	0.00	1.0000
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA}$	28	28.08	0.4603
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR}$	32	48.87	0.0285
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{jk}^{AR} + \lambda_{ij}^{MA}$	56	241.75	0.0000
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{ij}^{MA}$	35	125.03	0.0000

which implied that percent agreement was correlated to age-class and ageing method, and the estimated age frequencies differed by ageing method. However, these pairwise relationships between any two factors are unrelated to the third.

Because we are interested in the effects of ageing method and age class on repeatability, it is reasonable to look at the ratio between agreement ($k = 1$) and disagreement ($k = 2$) for each combination of ageing method and age class, i.e., m_{ij1}/m_{ij2} for all i and j. The logarithm of this ratio is known as the logit model (Fienberg 1981, chapter 6). The logit model for Equation (2) can be derived as

$$\text{logit}(i,j) = \log\,(m_{ij1}/m_{ij2}) = \omega + \omega_i^M + \omega_j^A \quad (3)$$

where, the logit effects, $\omega = (\lambda_1^R - \lambda_2^R)$, $\omega_i^M = (\lambda_{i1}^{MR} - \lambda_{i2}^{MR})$, and $\omega_j^A = (\lambda_{j1}^{AR} - \lambda_{j2}^{AR})$. The effects ($\lambda$'s) without factor R in Equation (2) are cancelled out by subtraction in Equation (3). The values of λ's can be obtained from the BMDP program and substituted into Equation (3). The results show that there was a significant declining effect on agreement as age increased (Table 4). This indicated that percent agreement decreased with increasing age. Age determination using coracoids and dorsal fin rays had a positive effect on agreement, which indicated that agreement of these methods was higher than the average of the five methods, but the other ageing methods had a negative effect, i.e., agreement was lower than average.

Table 5 shows that the effect of ageing method was significant for all fish older than age 3. There was no significant difference (5% level) between readings except for ages 5-6. This difference probably resulted from differences between readings for otoliths and pectoral fin rays (Table 6). Mean square (MS) for the ageing method effect increased with age and was the predominant component in the within-subject variation for all age categories. Therefore, variability in age determination was mainly due to ageing method rather than inconsistent annulus interpretation by the reader.

TABLE 4.—Estimated logit effects corresponding to the loglinear model in Equation (2).

Factor		Logit effect
constant (ω)		0.540
Age (ω_j^A)	≤2	2.204
	age 3	0.240
	age 4	0.676
	age 5	0.278
	age 6	−0.196
	age 7	−0.738
	age 8	−1.064
	over 9	−1.400
Age method (ω_i^M)	Dorsal fin ray	0.568
	Coracoid	0.096
	Otolith	−0.058
	Pectoral fin ray	−0.208
	Scale	−0.398

Using the Q-statistic, the mean ages of the two readings were not significantly different except for age group 5-6 using otolith and pectoral fin-ray ageing methods (Table 6). Significant differences between ageing methods were found in all age categories except the youngest. Age readings from dorsal fin rays and pectoral fin rays were not significantly different for fish younger than age 6. Age readings from otoliths and pectoral fin rays were not significantly different for fish older than age 7. Otolith readings were older than other methods for fish younger than age 6 but were younger than dorsal fin-ray readings for fish older than age 7. Scale readings gave consistently younger ages than the other methods.

Bakkala and Wespestad (1984) reported that recruitment of the 1977 year class was uniquely strong when compared to its neighboring year classes. The modal length of this year class can be

TABLE 5.—Comparison of ageing variability of Pacific cod by ANOVA.

Dorsal fin-ray age	N		Between subject (π)	Within subject					
				Method (M)	$M\pi$	Reading (R)	$R\pi$	MR	$MR\pi$
1-2	8	SS	14.359	0.297	2.578	0.016	0.109	0.047	1.328
		df	7	3	21	1	7	3	21
		MS	2.051	0.099	0.123	0.016	0.016	0.016	0.063
		F		0.81		1.00		0.25	
3-4	19	SS	52.395	8.967	38.658	0.164	3.711	0.072	7.553
		df	18	3	54	1	18	3	54
		MS	2.911	2.989	0.716	0.164	0.206	0.024	0.140
		F		4.18**		0.80		0.17	
5-6	93	SS	270.495	166.154	273.721	1.840	26.285	1.122	74.253
		df	92	3	276	1	92	3	276
		MS	2.940	55.385	0.992	1.840	0.286	0.374	0.269
		F		55.85**		6.44**		1.39	
7-8	57	SS	217.244	344.018	267.232	0.219	26.031	0.921	56.829
		df	56	3	168	1	56	3	168
		MS	3.879	114.673	1.591	0.219	0.465	0.307	0.338
		F		72.09**		0.47		0.91	
9+	23	SS	339.457	498.283	198.717	0.035	21.652	1.869	53.130
		df	22	3	66	1	22	3	66
		MS	15.430	166.090	3.011	0.348	0.984	0.623	0.805
		F		55.16**		0.35		0.77	

** = significant at 1% level.

TABLE 6.—Tests for differences between mean ages of Pacific cod using various ageing methods. Bracket and underline: not significantly different at 5% level.

Dorsal fin-ray age	N	Reading	Dorsal fin ray	Otolith	Pectoral fin ray	Scale	SD	df
1-2	8	1	1.375	1.375	1.375	1.250	0.063	7
		2	1.375	1.475	1.375	1.250		
		Method mean	1.375	1.425	1.375	1.250	0.124	21
3-4	19	1	3.842	4.211	3.842	3.579	0.147	18
		2	3.847	4.315	3.895	3.579		
		Method mean	3.895	4.263	3.869	3.579	0.194	54
5-6	93	1	5.505	5.774	5.430	4.581	0.078	92
		2	5.588	5.979	5.591	4.570		
		Method mean	5.547	5.877	5.511	4.576	0.103	276
7-8	57	1	7.386	6.561	6.614	5.000	0.128	56
		2	7.316	6.702	6.737	4.982		
		Method mean	7.351	6.632	6.676	4.991	0.167	168
9+	23	1	10.130	8.000	8.304	5.522	0.293	22
		2	9.913	8.261	8.130	5.304		
		Method mean	10.022	8.131	8.217	5.413	0.362	66

traced from the length-frequency distributions from 1978 to 1983 (Fig. 2). Using the method of Macdonald and Pitcher (1979), the mean lengths for ages 1-6 were 22, 35, 43, 52, 61, and 64 cm respectively (Lai 1985) and were very close to the modal length of length-frequency distributions. Figure 2 shows the mean lengths at age estimated from the 1983-84 samples by the five ageing methods and the comparison to the modal lengths. It is apparent that the mean lengths at age estimated from dorsal fin rays were closest to the modal lengths. Also, the variability around mean length at age estimated from dorsal fin rays was generally smaller than for the other methods. We also used the index of variation[6] (IV, Lai

[6] $IV = 100\% \cdot \sqrt{\Sigma(Y_i - X_i)^2/[(n-1)(\overline{X} + \overline{Y})/2]}$, where X_i is the first age reading, Y_i is the second age reading, n is the sample size, and $\overline{X}$ and $\overline{Y}$ are mean of the X_i and Y_i (Lai 1985). This indicates the degree of variation between the two

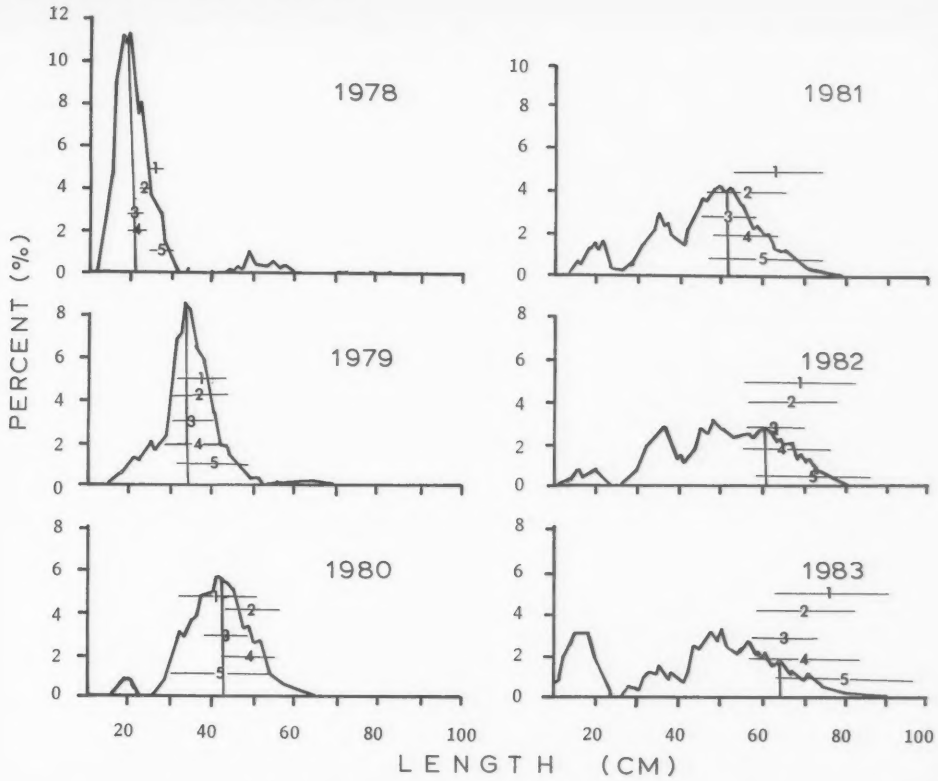

FIGURE 2.—Length-frequency distributions collected from trawl surveys in 1978-83 (after Bakkala and Wespestad 1984). The mode in 1978 represents age-1 Pacific cod of the 1977 year class, and progresses from age 2 to age 6 in the subsequent years. The estimated mean lengths at ages 1-6 estimated from the five ageing methods (1, coracoids; 2, otoliths; 3, dorsal fin rays; 4, pectoral fin rays; and 5, scales) correspond to the age of 1977 year class. Horizontal lines indicate 95% confidence interval around means. Vertical lines indicates the mean length from length-frequency analysis.

1985) to examine the degree of precision. Among the five ageing methods, the IV for dorsal fin rays was the lowest (13%) when compared with other methods (14%, 14%, 15%, and 16% respectively for otoliths, coracoids, scales, and pectoral fin rays).

The accuracy of converting scale ages to dorsal fin-ray ages was also evaluated. Mean length at age and age composition (obtained by using converted dorsal fin-ray ages) were compared with corresponding results from length-frequency analysis (Macdonald and Pitcher 1979). The 95% confidence interval (Fig. 3) for each converted mean length at age in 1979 and 1980 included the corresponding value estimated from the length-frequency analysis. However, the mean lengths at age derived from scales were significantly different from the other two.

The age composition estimated by the scale method showed a monotonic decrease with age in 1979, and the strong 1977 year class (age 2) was not evident (Fig. 4). Nevertheless, length-frequency data from surveys indicated that age-2 fish were dominant in 1979 (Bakkala and Wespestad 1984). The age composition based on converted dorsal fin-ray ages was dominated by age-2 fish and was similar to that estimated from the

ages being compared taking the age distribution of the sample into account.

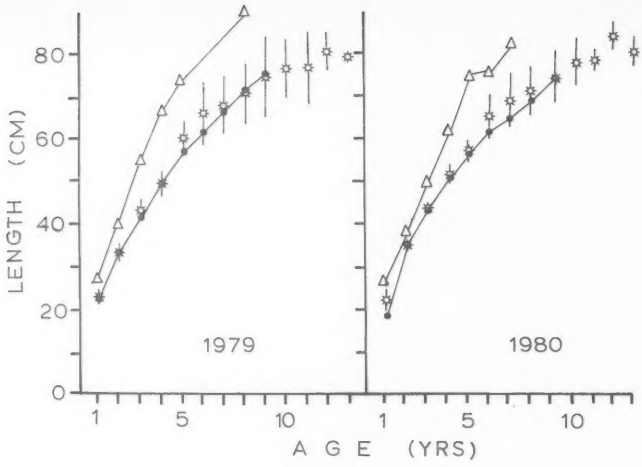

FIGURE 3.—Comparison of mean length at age estimated from scales (—Δ—), converted dorsal fin-ray ages (*), and length-frequency analysis (—●—) for 1979 and 1980. Vertical line indicates the 95% confidence interval from the 30 simulation runs.

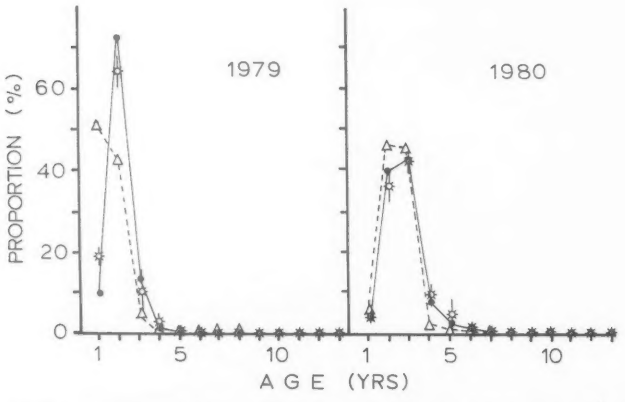

FIGURE 4.—Comparison of age composition estimated from scales (—Δ—), converted dorsal fin-ray ages (*), and length-frequency analysis (—●—). Vertical line indicates 95% confidence interval of the 30 simulation runs.

length-frequency analysis. In 1980, the proportions estimated by using the scale method were somewhat higher than for the other two methods at ages 2 and 3 (Fig. 4), but were lower at ages 4 and 5. Since the classification probabilities and scale age-length keys used in this study were derived independently from different years, the method of age conversion appears to be relatively insensitive to interannual differences in the classification probabilities.

DISCUSSION

Although Westrheim and Shaw (1982) validated the interpretation of the annuli on scales for age groups 1 and 2, this validation was not

considered to be sufficient for all age groups. Beamish et al. (1978, figs. 12 and 13) showed that the difference between readers was substantial even in age groups 1 and 2. In our study, we found that age readings from the scale method had low precision, and that scale ages were much younger than those obtained by any other method.

In this study, validation for age groups 1-6 showed that dorsal fin rays gave the most reliable ages for Pacific cod and thus should be used in the future. This method provided estimates of mean length at age that agreed most closely to observed growth of the 1977 year class, and the precision of this method was the highest attained in this study. Another major advantage of this ageing method is that additional fin rays can be taken from fish with a previous history of fin-ray removal to verify the accuracy of age determinations between time of release and recapture.

We used the Monte Carlo method to convert scale ages to dorsal fin-ray ages. The results indicated that the previously collected scale age data can be used in age-dependent methods of stock assessment. Since the 1983-84 classification probabilities used in this study were completely independent of the 1979-80 scale age data, the method appears to be robust with respect to interannual variability in the classification probabilities for Pacific cod. However, application of this method to other species will require caution when the classification probabilities are applied to the data from different years, since interannual variability could be a source of error. Still, any errors that arise will probably be smaller than those produced from an inappropriate ageing method.

Analytical methods, such as those of Pella and Robertson (1979) and Cook (1982), could also be used for converting scale age-length keys to dorsal fin-ray age-length keys. However, these methods are mathematically more complicated and occasionally yield negative values in some of the converted age-length keys (Cook 1982). The method of Hoenig and Heisey (1987)[7] is of particular interest because it avoids negative values by applying an incomplete E-M (estimation and maximization) algorithm to fit a log-linear model to the classification matrix. Nevertheless, this method may not be valid if there is a substantial systematic ageing error (as in our case, dorsal fin-ray ages vs. scale ages) because too many empty cells are in the classification matrix. Alternatively, the method of Barlow (1984) can also be used for this purpose, although the result will be very similar to our Monte Carlo method, as Barlow's method is a deterministic version of our own.

[7]Hoenig, J. M., and D. M. Heisey, 1987. Using log-linear models with the EM algorithm to correct estimates of stock composition and convert to age. Manuscr. in prep. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL.

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APPENDIX A.—ANALYSIS BY LOG-LINEAR MODEL

In our study, there are three factors, ageing method (M), age class (A), and repeatability (R). Our sampling model is product-multinomial, using the terminology of Fienberg (1981, Sec. 3-2), since the number of fish being aged is fixed for each ageing method after deleting unreadable or damaged age-structures. The aged fish were cross-classified into corresponding cells denoted by factors A and R (Table 1).

Let y_{ijk} be the observed cell frequency for the ith ageing method, the jth row of age class, and the kth column of repeatability, and let m_{ijk} be the expected value of y_{ijk}. The general log-linear model (called the saturated model because it includes the highest three-factor interaction) for our three-way ($5 \times 8 \times 2$) contingency table is

$$\theta_{ijk} = \log(m_{ijk}) = \mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA} + \lambda_{ijk}^{MAR} \tag{A.1}$$

where, as in the usual analysis of variance model, all effects sum up to zero over any subscript. Let $\bar{\theta}$ be the marginal mean of θ_{ijk} over the subscript which is replaced by "+" to indicate averaging, then the parameters in (Equation A.1) can be written as

$$\begin{aligned}
\mu &= \bar{\theta}_{+++} & \lambda_{ij}^{MA} &= \bar{\theta}_{ij+} - \bar{\theta}_{i++} - \bar{\theta}_{+j+} + \bar{\theta}_{+++} \\
\lambda_i^M &= \bar{\theta}_{i++} - \bar{\theta}_{+++} & \lambda_{ik}^{MR} &= \bar{\theta}_{i+k} - \bar{\theta}_{i++} - \bar{\theta}_{++k} + \bar{\theta}_{+++} \\
\lambda_j^A &= \bar{\theta}_{+j+} - \bar{\theta}_{+++} & \lambda_{jk}^{AR} &= \bar{\theta}_{+jk} - \bar{\theta}_{+j+} - \bar{\theta}_{++k} + \bar{\theta}_{+++} \\
\lambda_k^R &= \bar{\theta}_{++k} - \bar{\theta}_{+++} & \lambda_{ijk}^{MAR} &= \bar{\theta}_{ijk} - \bar{\theta}_{ij+} - \bar{\theta}_{i+k} + \bar{\theta}_{i++} \\
& & & \quad - \bar{\theta}_{+jk} + \bar{\theta}_{+j+} + \bar{\theta}_{++k} - \bar{\theta}_{+++}.
\end{aligned} \tag{A.2}$$

Log-linear models are "hierachical", i.e., higher-order interaction terms can be included only if related lower-order terms are included. For example, λ^{MAR} is not included unless λ^{AR}, λ^{MR}, and λ^{MA} are all included.

Once all expected cell frequencies (m'_{ijk}) are estimated, the goodness-of-fit for the selected model can be tested using the likelihood ratio test statistic

$$G^2 = 2 \sum_i \sum_j \sum_k y_{ijk} \log \left(\frac{y_{ijk}}{m'_{ijk}} \right) \tag{A.3}$$

which has approximately a χ^2 distribution with degrees of freedom (df) = number of cells − number of parameters (Fienberg 1981, sec. 3-3 and 3-4).

Using the partition property of G^2, we can decide whether an effect or an interaction should be included. In Table 3, for example, H_0: $\lambda^{MAR} = 0$ can be tested by examining $G^2 = 28.08 - 0.00 = 28.08$. This is not significant at the 1% level (referred to a χ^2 distribution with df = 28). Similarly, $G^2 = 20.79$ for H_0: $\lambda^{MA} = 0$, which exceeds the upper 1% tail value of a χ^2 distribution with df = 4, and is rejected. This means that λ^{MAR} will not be included in the model but λ^{MA} will. Hence, our best log-linear model is Equation (2).

SIDESCAN SONAR AS A TOOL FOR DETECTION OF DEMERSAL FISH HABITATS

K. W. ABLE,[1] D. C. TWICHELL,[2] C. B. GRIMES,[3] AND R. S. JONES[4]

ABSTRACT

Sidescan sonar can be an effective tool for the determination of the habitat distribution of commercially important species. This technique has the advantage of rapidly mapping large areas of the seafloor. Sidescan images (sonographs) may also help to identify appropriate fishing gears for different types of seafloor or areas to be avoided with certain types of gears. During the early stages of exploration, verification of sidescan sonar sonographs is critical to successful identification of important habitat types. Tilefishes (*Lopholatilus* and *Caulolatilus*) are especially good target species because they construct large burrows in the seafloor or live around boulders, both of which are easily detectable on sonographs. In some special circumstances the estimates of tilefish burrow densities from sonographs can be used to estimate standing stock. In many localities the burrow and boulder habitats of tilefish are shared with other commercially important species such as American lobsters, *Homarus americanus;* cusk, *Brosme brosme*; and ocean pout, *Macrozoarces americanus*.

Acoustic techniques have become important tools in fishery research in the last 20 years. Of these, sonar has proven useful in a number of related efforts for pelagic fisheries (Forbes and Nakken 1972) including the detection of fishes in the water column (Harden-Jones and McCartney 1962; Anderson and Zahuranec 1977) and estimation of fish numbers and biomass (Smith 1970; Hewitt et al. 1976; Suomala and Lozow 1980; Barans and Holliday 1983; Nakken and Venema 1983). More recent studies have demonstrated how sidescan sonar, in combination with acoustically tagged fish, can be used to evaluate trawling gear (Harden-Jones 1980). Sidescan sonar has been used infrequently to assess critical habitat for demersal fishery resources with the exception of an early attempt to map a herring (*Clupea harengus*) spawning area (Stubbs and Lawrie 1962). Our research has focused on detection of tilefish burrows (Twichell et al. 1985; Grimes et al. 1986; Able et al. 1987), but an outgrowth has been the identification of the habitats of other species. Here we describe the use of sidescan sonar to map the extent and distribution of different habitat types and, in the case of tilefish, derive an estimate of standing stock and potential yield.

TECHNIQUE

Sidescan sonar is similar to low-angle, oblique, aerial photography except that the images (sonographs) are based on differences in the intensity of the reflected acoustic signal rather than the intensity of the reflected light (Belderson et al. 1972). The system consists of a towed vehicle (Fig. 1) in which is housed two sets of transducers that scan to each side, a conducting tow cable, a winch, and a dual-channel recorder for displaying the signals. The transducers are constructed so that their beams form a very narrow arc (1-2°) in the direction perpendicular to the ship's track, but a broad arc in the direction parallel to the ship's track (Fig. 1). As the ship moves, successive bands of seafloor are insonified, and in this way an acoustic areal map is recorded of the scanned area.

We used a 100 kHz Klein[5] sidescan sonar system. This system can resolve features as small as 0.5 m diameter (see Results) at a scanning range of 100 m to each side of the towed vehicle. The

[1]Center for Coastal and Environmental Studies and Department of Biological Sciences, Rutgers University, New Brunswick, NJ 08903; present address: Marine Field Station, Rutgers University, Tuckerton, NJ 08087.
[2]U.S. Geological Survey, Woods Hole, MA 02543.
[3]Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, Panama City, FL 32407.
[4]University of Texas Marine Science Institute, Port Aransas, TX 78373.

[5]Use of trade names in this report does not constitute endorsement by the U.S. Geological Survey or the National Marine Fisheries Service.

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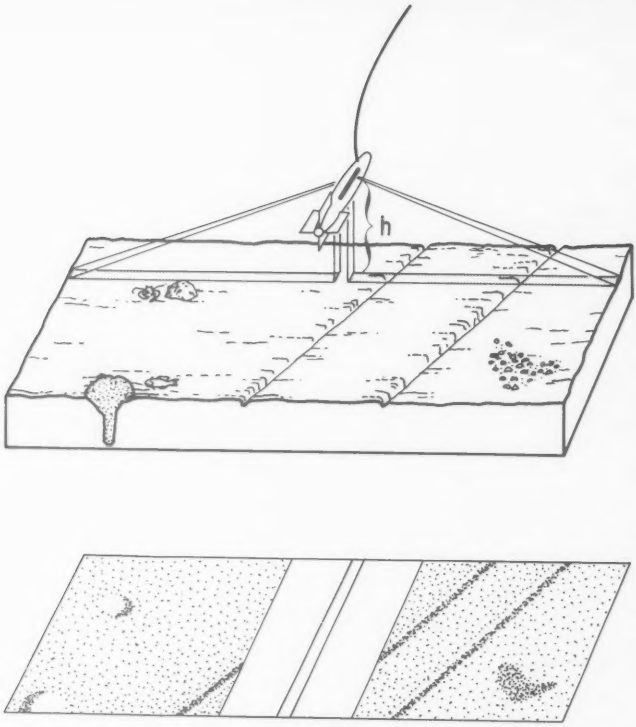


FIGURE 1.—Schematic diagram of a sidescan sonar vehicle being towed over the seafloor (upper) and resulting sonograph (lower) with images of trawl door tracks, tilefish burrow, gravel, and a boulder.

sidescan vehicle was towed 10-15 m above the seafloor at speeds of 3-7 km/hour and was set to scan 100 m or 150 m to each side of the towed vehicle. At these speeds and scanning range, 0.6-1.4 km^2 of seafloor could be mapped per hour.

The sidescan sonograph signatures that characterize different habitat types are largely determined by two conditions, topography and fine-scale roughness (in particular, differences in sediment texture). The signals received from tilefish burrows (Fig. 2) and boulders (Fig. 3) provide good examples of differences in strength of the recorded signal due to topographic effects. A strong signal (dark) is received from the side of the feature facing the transducer while a weak signal or shadow (light) is received from the side sloping away from the transducer. Thus, boulders have the strong return nearest the transducer followed by a shadow (Fig. 3), while burrows appear as a shadow preceding the strong return (Fig. 2). Gravel gives a much stronger signal than silt because of the many small facets facing the transducers. Textural differences usually can be distinguished from topographic differences because there is no shadow associated with them (Fig. 4).

Although the sonograph is a map view of the seafloor, there are two distortions that must be compensated for when interpreting these images. The first is the across-track, slant-range distortion which results from distances being measured from the sidescan vehicle that is positioned above the bottom and not the zero line on the seafloor below the towed vehicle (Fig. 1). For this reason, the point on the seafloor directly below the fish is plotted away from the actual zero line by the distance the fish is off the bottom (distance h on Figure 1). The second geometric distortion is in

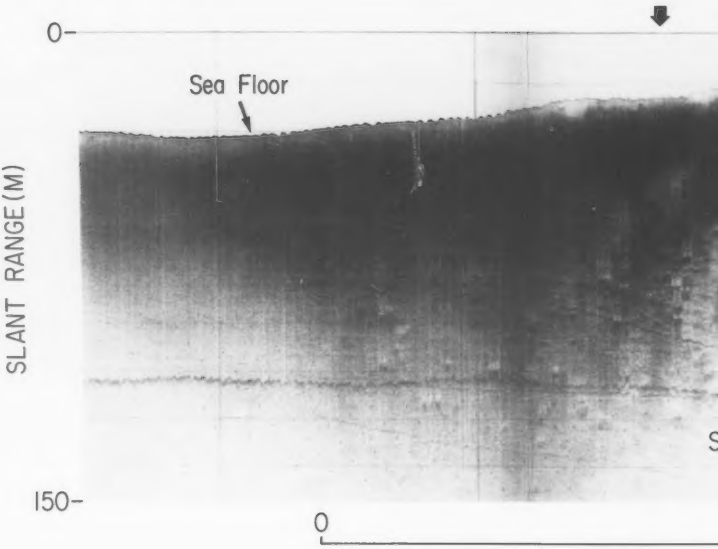
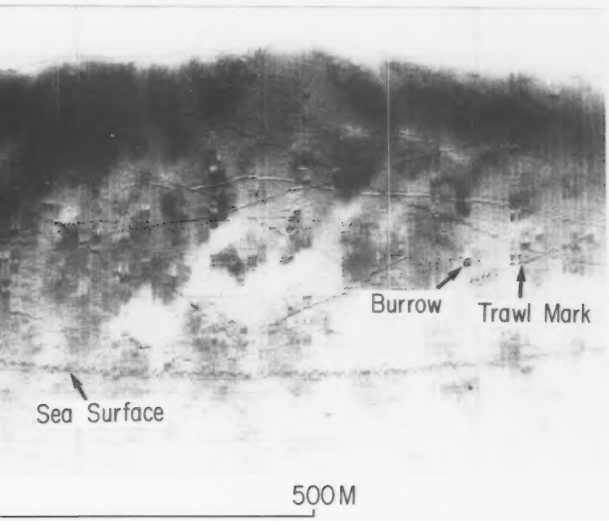


FIGURE 2.—Sidescan sonograph of seafloor with vertical burrows of tilefish, *Lopholatilu*
arrow denotes direction of incomi



olatilus chamaeleonticeps, and trawl door tracks in substrate. Heavy
incoming sound.

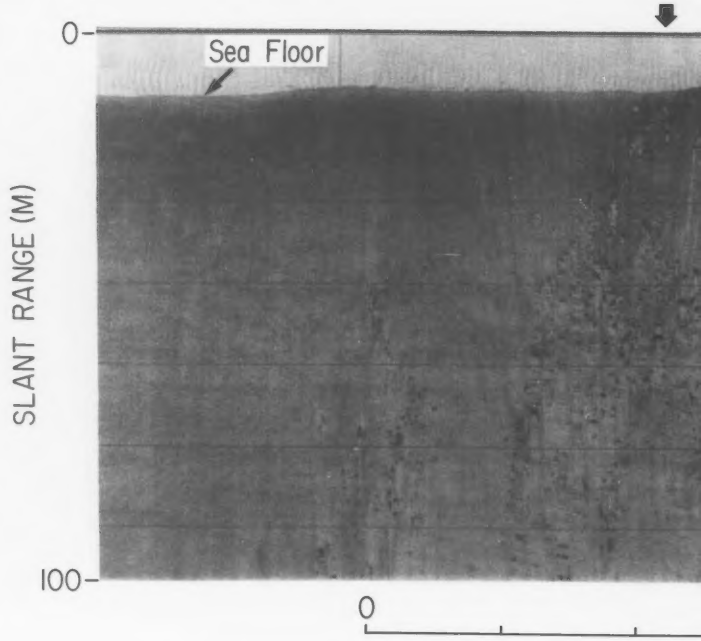
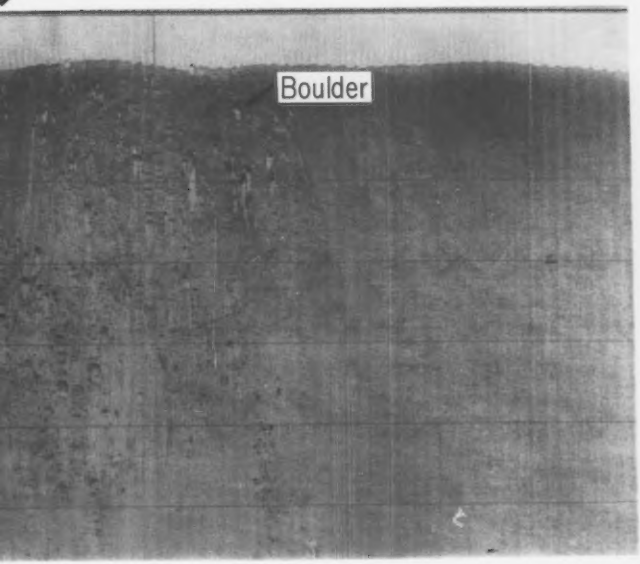


FIGURE 3.—Sidescan sonograph of seafloor in Vineyard Sound with bould
sour



n boulders resting on the substrate. Heavy arrow denotes direction of incoming sound.

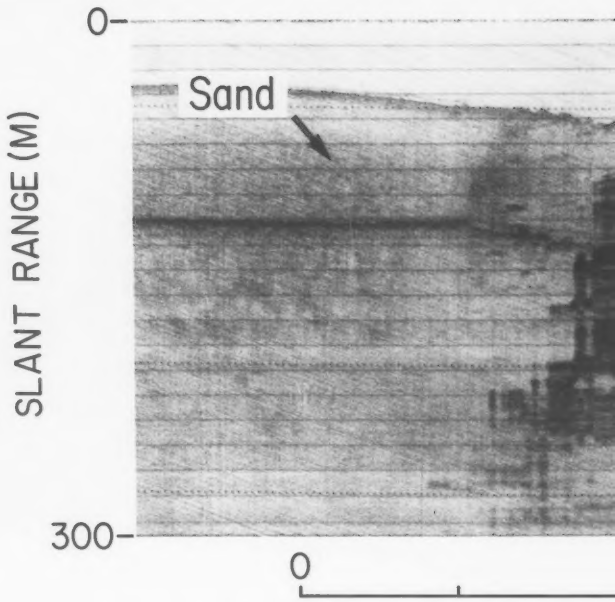
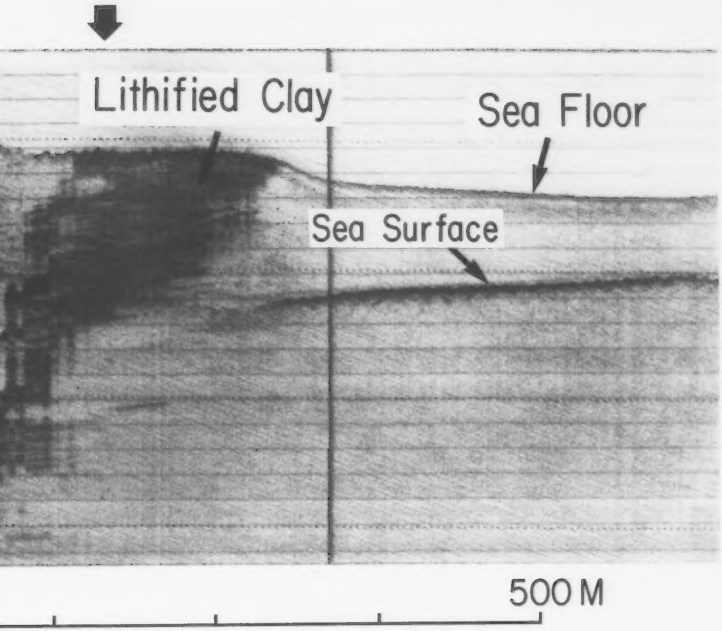


FIGURE 4.—Sidescan sonograph of Lydonia Submarine Canyon wall wit
and American lobster. Heavy ar



vall with outcrop of lithified, burrowed clay likely to be site of pueblo habitat of tilefish
avy arrow denotes direction of incoming sound.

the along-track direction and is due to the ship's speed. Normally the records are compressed in the direction the ship travelled relative to the true geometry. A circular feature will look elliptical on the sonograph, with the long axis of the ellipse perpendicular to the ship's track, and a linear feature will look more perpendicular to the track than it really is.

RESULTS AND DISCUSSION

The Tilefish Example

Our initial discovery (Able et al. 1982) that tilefish, *Lopholatilus chamaeleonticeps*, construct large (up to 4-5 m diameter and 2-3 m deep), vertical burrows in the substrate (Fig. 5A) suggested that we might be able to detect these burrows with sidescan sonar. Since then we have successfully determined tilefish occurrence, distribution patterns, and relative abundance based on sidescan sonar observations at the edge of the continental shelf in the Mid-Atlantic Bight (Twichell et al. 1985; Grimes et al. 1986) and the upper slope off Florida (Able et al. 1987) (Table 1). Verification of sonograph images as tilefish burrows (Figs. 2, 5A) was accomplished by in situ observations from the *Johnson-Sea-Link* submersibles (Askew 1985) (Table 1).

As a result of these studies, we have demonstrated that sidescan sonar can consistently detect tilefish burrows both where the substrate consists of semilithified clay (Mid-Atlantic Bight: Twichell et al. 1985; Grimes et al. 1986) and softer carbonate muds (off east coast of Florida; Able 1987). During sidescan and submersible operations near Veatch Submarine Canyon, we determined that sidescan sonar could detect tilefish burrows as small as 0.5 m in diameter. Detection of small burrows on sidescan was confirmed when burrows in the area were measured in situ and found to be 35-65 cm in diameter (mean = 48 cm, sample number = 8).

TABLE 1.—Sidescan sonar observations of tilefish, *Lopholatilus* and *Caulolatilus*, burrows on the seafloor off the east coast of the United States.

Location	Date	Sidescan trackline distance (km)	Depth range (m)	No. of verification dives
Vicinity of Hudson Submarine Canyon, Mid-Atlantic Bight	July 1982; August 1983	100	90-200	6
Between Block and Veatch Submarine Canyons, Mid-Atlantic Bight	July-August 1984	129	100-350	2
Off Cape Canaveral, FL	May 1984	36	100-250	2

Under certain situations, tilefish abundance could be estimated directly from sonographs. Usually one tilefish is associated with each burrow (Able et al. 1982), therefore sidescan sonograms providing burrow counts could be used to estimate standing stocks in areas surveyed, with a modification of the area-density method (Everhardt and Youngs 1981). Frequency distributions of burrow density per unit area were log-normal, and there were considerable numbers of zero observations (i.e., about 14-24% zero observations). Therefore we $\log_e$ transformed the burrow density data, and calculated the sample mean and variance of the delta distribution according to Pennington (1983). We present sample estimates from our data for two different locations:

Case 1: Middle Atlantic Bight in the vicinity of Hudson Submarine Canyon (number of observations = 407, number of nonzero observations = 316, data from Twichell et al. 1985) based on the formula

$$N = \frac{B}{a} \cdot A$$

where N = total number of fish (burrows) in surveyed area, $\frac{B}{a}$ = delta-distribution mean number of burrows observed per unit area surveyed, A = total area surveyed, SD = standard deviation, and C.I. (confidence interval) = 95% (1.96 × SD) calculated from the delta-distribution variance, thus

$$N = \frac{2{,}558}{\text{km}^2} \cdot 0.407\ \text{km}^2 \text{ with SD} = 123 \text{ and } 95\%$$

C.I. = 241

$N = 1{,}041 \pm 98$ tilefish [in the surveyed area].

Case 2: South Atlantic Bight off Ft. Pierce, FL (number of observations = 46, number of nonzero observations = 40). The data was obtained with 167 kHz sidescan sonar from the research submersible NR-1 (Able et al. unpubl. data). In this instance

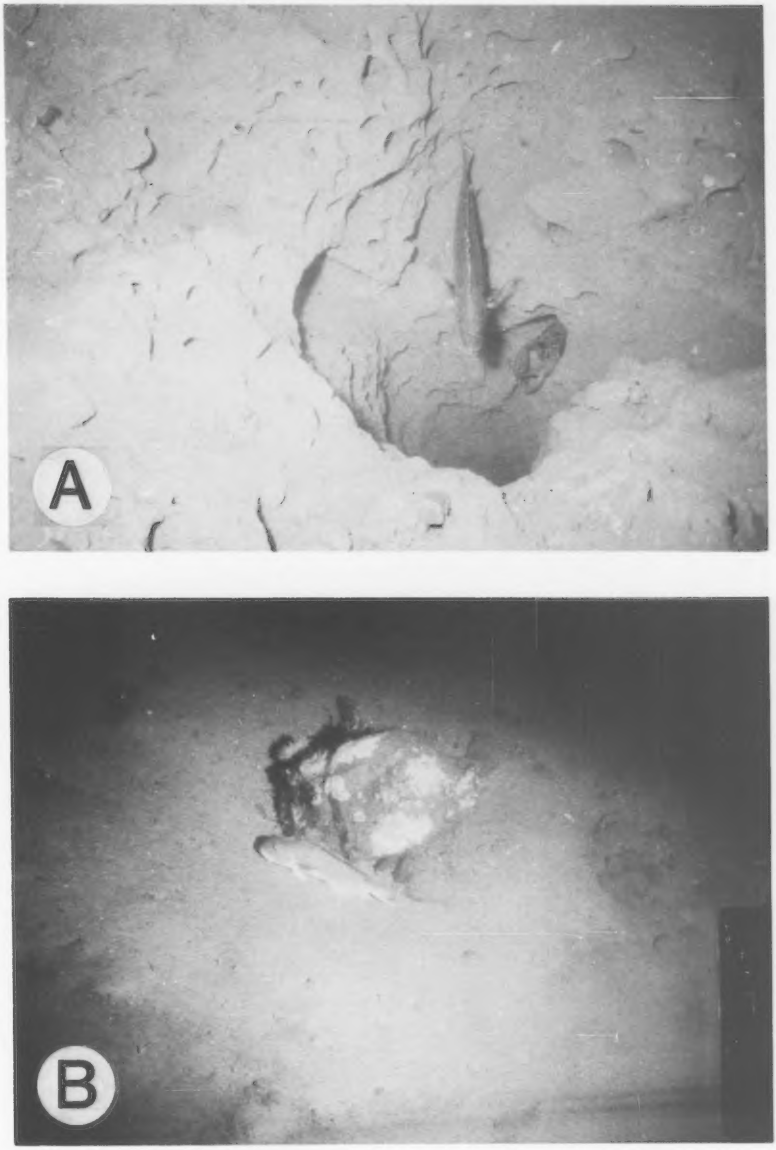


FIGURE 5.—Photographs of A) tilefish, *Lopholatilus chamaeleonticeps*, and American lobster, *Homarus americanus*, in a vertical burrow, and B) tilefish in boulder habitat. These are the same kind of habitats shown as sidescan sonographs in Figures 2 and 3 respectively.

$$N = \frac{369}{\text{km}^2} \cdot 0.42 \text{ km}^2 \text{ with SD} = 64 \text{ and } 95\% \text{ C.I.}$$

$$= 125$$

$N = 154 \pm 53$ tilefish [in the surveyed area].

The estimates of N in cases 1 and 2 could be extrapolated to the entire fishing grounds using an estimate of the area of the entire grounds to provide an estimate of standing stock. However, we believe that extrapolation to areas where no density data is available is imprudent for several reasons. First, the density of burrows in different locations is quite variable as shown in the two above examples, and density on the Middle Atlantic-Southern New England ground (case 1) varies over the grounds at least tenfold (Grimes et al. 1986). Second, some burrows, at least in the Middle Atlantic-Southern New England area, may not be occupied during all seasons of the year (Grimes et al. 1986). Although we do not have as much background knowledge for case 2, we know that burrow density at different sites off the Florida east coast varied at least fivefold (Able et al. unpubl. data).

Another possible source of error in using burrow density to estimate tilefish stock size is that some burrows may be unoccupied. This should be of particular concern in exploited fishing areas. However, Twichell et al. (1985) and Able et al. (unpubl. data) have shown that abandoned burrows are filled by sedimentation relatively rapidly, i.e., less than one year, somewhat ameliorating the problem, at least over longer time periods.

Perhaps the most constructive aspect of cases 1 and 2 is the opportunity to examine the error associated with sidescan sonar estimates of N. These results show that the standard deviation varied from about 5 to 20% of the mean. Hennemuth (1976) found that the standard deviation in the numbers of different demersal species caught per tow within a stratum during stratified bottom trawl surveys approximately equalled the mean. Thus, this comparison suggests that area density estimates of abundance (calculated using the delta distribution) from sidescan sonar surveys will provide abundance estimates of much greater precision than trawl surveys. Reduced manpower needs and rapid application are additional factors that favor the sidescan sonar methodology. However, because the sidescan methodology is only useful for certain three dimensional habitats (e.g., reefs, rocks, and burrows) that would damage or make a trawl useless, application of the two techniques may usually be mutually exclusive.

Tilefish are known to occur in other habitats (Grimes et al. 1986) such as boulder fields, which can be detected on sidescan sonographs (Figs. 2, 5B). Another habitat type (pueblo habitats, Warme et al. 1977; Grimes et al. 1986) occurs in the clay outcrops along the walls of submarine canyons (Figs. 4, 6A). Neither of these habitat types lend themselves to quantification of fish abundance. Recently, we have been able to confirm that the burrows of other tilefish (*Caulolatilus* spp.) are also detectable with sidescan sonar (Able et al. 1987; Figs. 6B, 7). Subsequent observations from a submersible confirmed that these burrows were occupied by *C. microps* and *C. cyanops* with frequent multiple occupancy. Given that it has now been demonstrated that representatives of four of the five genera of tilefishes construct burrows (see Able et al. 1987), it is reasonable to suspect that all tilefish construct burrows. Thus, those larger species of commercial interest, such as red tilefish, *Branchiostegus japonicus japonicus* (Lim and Misu 1974), also may have burrows that are detectable by sidescan sonar.

Other Examples and Possibilities

As an outgrowth of our studies of *Lopholatilus* we have observed other species-specific habitats that can be detected with sidescan sonar. American lobster, *Homarus americanus,* typically occupy scour basins around large boulders (Cooper and Uzmann 1977; Valentine et al. 1980) as do cusk, *Brosme brosme,* and ocean pout, *Macrozoarces americanus* (Valentine et al. 1980; Grimes et al. 1986), and these habitats also are detectable with sidescan sonar. American lobster (Fig. 5) and conger eels, *Conger oceanicus,* (Able et al. 1982; Grimes et al. 1986) have been observed in tilefish vertical burrows as well. Similarly, it would not be surprising if the habitats of other clawed lobsters are detectable with sidescan sonar. For example, *H. gammarus* from the eastern North Atlantic is similar to *H. americanus* in that it is shelter seeking and occurs around boulders (Dybern 1973). In addition, recent in situ observations in the Gulf of Mexico have discovered that yellowedge grouper (*Epinephelus flavolimbatus*) also occupy burrows and elongate trenches (R. S. Jones, E. Gutherz, and W. R. Nelson, pers. obs.) that could easily be detected by sidescan sonar.

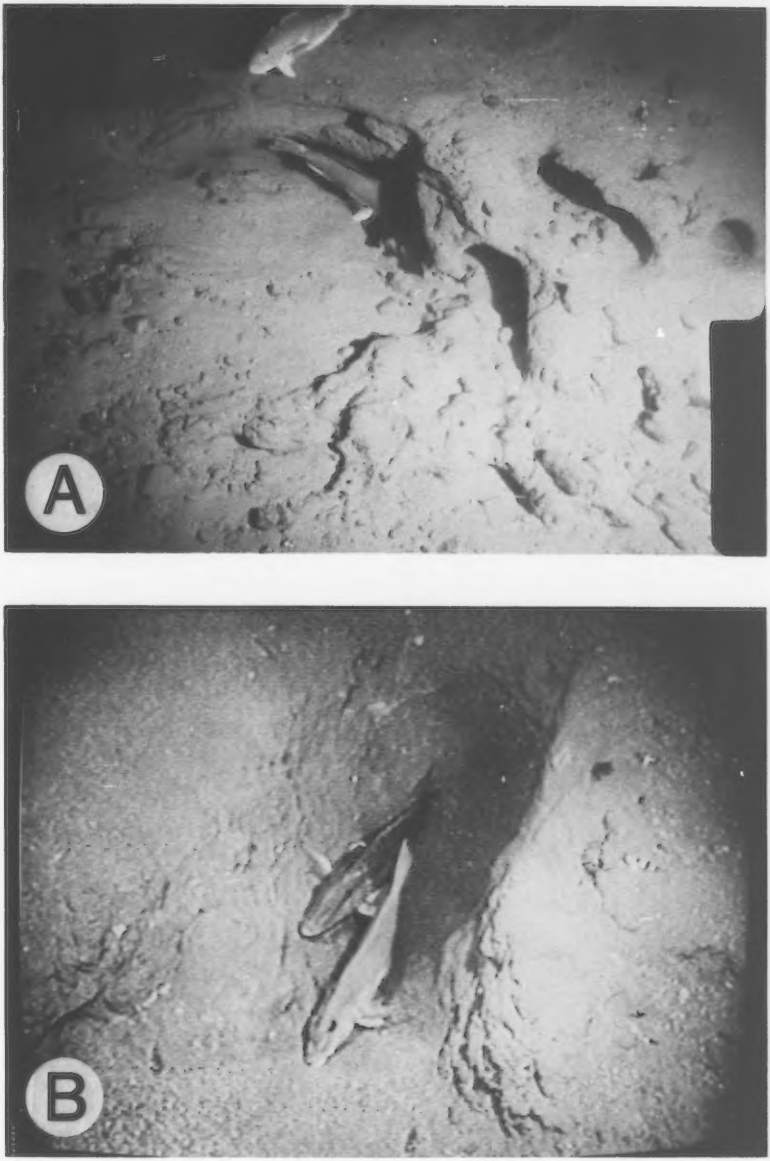


FIGURE 6.—Photograph of tilefish, *Lopholatilus chamaeleonticeps*, in A) pueblo habitat that is part of a clay outcrop and B) *Caulolatilus* tilefish in a burrow. These are the same kind of habitats as shown in Figures 4 and 7 respectively.

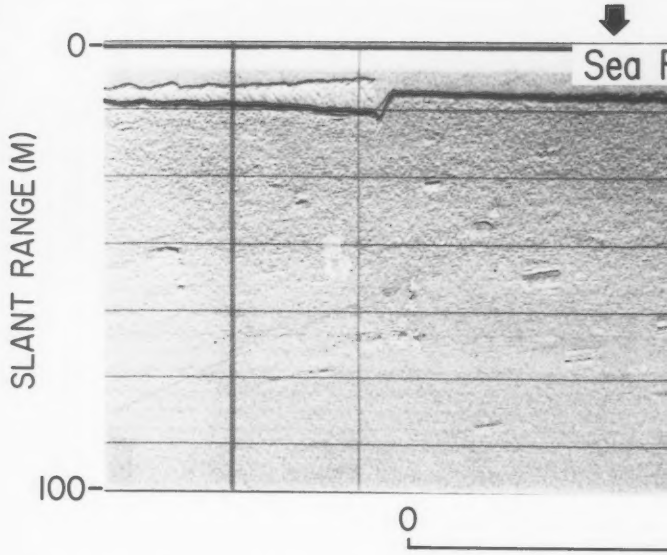
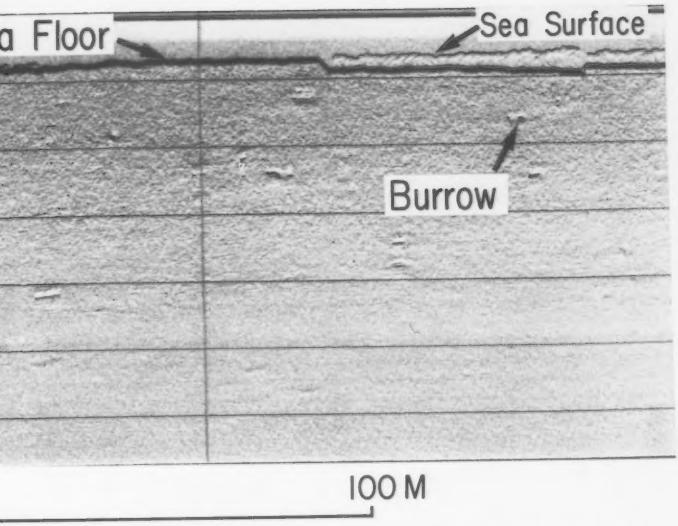


FIGURE 7.—Sidescan sonograph of seafloor with *Caulolatilus* tilefish burrows off Cape Can
or lowered. Heavy arrow denotes d



pe Canaveral, FL. The sharp steps in the seafloor trace are where the sidescan was raised
notes direction of incoming sound.

With sidescan sonar, detection and mapping of general habitat types such as rock outcroppings and wrecks, which support populations of commercially important species (e.g., Grimes et al. 1982; Sedberry and Van Dolah 1984), could be done efficiently. Sidescan sonar also could prove very effective (see Wong et al. 1970) in mapping the distribution and relief of a coral reef, and other outcroppings which are often the habitats of groupers, snappers, porgies, and grunts.

In addition to these specific examples, general characteristics of sidescan sonar are advantageous in detecting demersal fish habitats. The system has a wide effective search image (up to 150 m to each side for the 100 kHz Klein sidescan unit) that enables it to map large areas of the bottom during a single transect. With multiple transects a complete picture of the bottom can be obtained. Also, a sonograph could determine potentially appropriate habitats for several species simultaneously. For example, in our studies we have been able to detect boulders (potential lobster, tilefish, and cusk habitat) and vertical burrows (potential tilefish, lobster, and conger eel habitat) in the same transect of the sidescan sonar.

Verification of the various images that appear on the sonograph is critical to successful operation of sidescan sonar for fish habitat detection. We have been able to do this using observations from the *Johnson-Sea-Link* submersibles (Twichell et al. 1985; Grimes et al. 1986; Able et al. 1987). However, this is an expensive option and not generally available. Others have been able to verify sonograph targets from underwater photographs (Bouma and Rappeport 1984) or underwater television (Powles and Barans 1980). The simplest technique, and one that would offer the most information to a fishermen, is directed fishing at the location of sonograph targets of particular interest.

Even with these advantages, sidescan sonar operations are still expensive. However, a considerable body of sonograph data already exists that has not been utilized by fishermen or fishery biologists. A large number of sidescan sonar surveys have been conducted in North American waters in recent years, largely as a result of exploration for oil and related impact studies (Carpenter and Roberts 1979; Neurauter 1979; Carpenter et al. 1982). We have taken advantage of one of these surveys to identify possible tilefish burrows off the west coast of Florida, an area in which we had no prior experience. Individual burrows were clearly visible on sonographs (Neurauter 1979; target type No. 3, fig. 39) originally made to identify geologic bedforms.

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THE EFFECTS OF BOTTOM TRAWLING ON AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, IN LONG ISLAND SOUND

ERIC M. SMITH AND PENELOPE T. HOWELL[1]

ABSTRACT

American lobsters taken in the commercial trawl fishery in Long Island Sound, U.S.A., were inspected for incidence of damage and immediate mortality associated with bottom trawling. Similar sampling was conducted in the pot fishery. American lobsters from trawl and pot catches were held in controlled conditions for 14 days to determine the level of delayed mortality associated with the two fisheries. Trawl-caught lobsters were exposed to subfreezing (−9.5°C) temperatures for periods from 30 to 120 minutes and then returned to seawater to determine the rate of freeze-induced mortality. Major damage rates due to trawling ranged from 12.6-14.0% during molting periods to 0-5.6% during intermolt periods. Delayed mortality ranged from 19.2% during the July molt to 1% during August and appeared to be related to the incidence of damage, molt condition, and temperature. Mortality of American lobsters held in subfreezing temperatures occurred after 30-minute exposure and reached 100% at 120-minute exposure.

The American lobster, *Homarus americanus*, supports one of the most valuable commercial fisheries in the northwest Atlantic Ocean with landings of approximately 20,900 t per year valued at $115 million (Anonymous 1985). The fishery is conducted predominantly with traps or pots and, secondarily, with bottom trawl nets.

Long Island Sound is a 2,908 km^2 embayment of the Atlantic Ocean in southern New England, lying between Connecticut and New York at approximately lat. 41°N. The Sound supports a spawning stock of American lobsters and a valuable commercial lobster fishery, which, in 1985, generated landings of 1,134 t valued at $7.0 million for some 900 commercial fishermen. In Connecticut, over 90% of the commercial landings are taken by the pot fishery, and over 90% of Connecticut's commercial fishermen are lobster pot fishermen. Connecticut trawlers, who catch American lobsters in a mixed species bottom fishery, take <10% of Connecticut commercial landings and constitute about 10% of all commercial fishermen taking lobsters. Recreational lobstermen, both potters and scuba divers, totaled 2,440 in 1985 but only accounted for about 5% of total landings (CT DEP[2]).

The resource is heavily exploited with annual exploitation rates ranging from 85 to 95% (Briggs 1985; Blake 1986). Principal management measures include prohibitions on the taking of females bearing external eggs and the retention of any American lobster <81 mm carapace length (CL). These measures are intended to protect American lobsters from exploitation until they have reproduced at least once.

During late 1982, commercial catch per unit effort rates doubled from those of the previous 5 years (CT DEP fn. 2). This increase stimulated a shift in directed fishing by some trawlers from mixed finfish to lobsters. The redirection of effort also generated competition for lobsters and fishing space, and an extremely emotional controversy arose between potters and trawlers. This paper addresses the resource considerations of the controversy, that is, the impacts of mobile trawl gear on lobsters.

This study was designed to measure 1) the physical injury and immediate mortality incurred by American lobsters in the trawl fishery; 2) the potential level of trawl-induced delayed mortality of American lobsters less than the minimum length upon return to the water; and 3) the rate of mortality of American lobsters due to exposure to subfreezing air temperatures during winter fishing.

METHODS

Incidence of Damage

Biologists made 63 trips aboard commercial stern trawlers from 12 to 26 m and 12 trips on pot vessels from 12 to 14 m. Except during January

[1]Bureau of Fisheries, Connecticut Department of Environmental Protection, P.O. Box 248, Waterford, CT 06385.

[2]Connecticut Department of Environmental Protection (CT DEP) unpublished fishery statistics.

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1984, trawl samples were obtained each month from July 1983 through January 1985 during tows of 1-3 h duration. Similar observations of trawl catches were obtained from cruises made by the CT DEP's research vessel (a 13 m stern-rigged trawler) from May through November in 1983 and 1984 during tows of 0.5-2 h duration. Commercial pot fishery sampling was conducted intermittently during summer and fall in both years. All samples were obtained in Long Island Sound west of long. 72°52′W.

American lobsters were examined for evidence of physical damage, denoted as "new" (resulting from the current net tow or pot haul) or "old" (previously sustained). Old damage was inferred by the presence of discolored and healed tissue and by the absence of bleeding. New damage was further categorized as "major" and "minor". Major damage was defined as death, broken or crushed body parts or claw(s), and multiple injuries, even when each individual wound was minor. Minor injury included walking leg loss or damage, antenna damage, minor breakage to a claw or rostrum tip, and recently autotomized claw(s). Recent autotomy (reflex amputation) was defined as a fresh partition without discoloration of the covering membrane at the "breaking plane" (Herrick 1909). Additional data were recorded on length, sex, shell hardness, presence of eggs, and absence of claws. Soft, newshell, and hardshell condition generally followed stages A, B, and C, respectively, as described by Passano (1960). In this paper, the term "newshell" includes both soft and newshell lobsters (stages A and B).

In comparing damage rates between commercial and research vessels, we found that hardshell American lobsters <81 mm CL were damaged more frequently in research than in commercial samples ($\chi^2 = 6.143$). Since the research vessel used a smaller mesh (51 mm cod end) than commercial vessels (75-114 mm cod end), it caught a proportionately greater number of American lobsters <81 mm CL (86% research vs. 72% commercial). Therefore, only lobsters ≥81 mm CL were analyzed because the greater proportion of sublegal American lobsters and other biota in the small mesh sample might have resulted in an overestimate of damage relative to the commercial fishery, due both to intraspecific, agonistic behavior and to compacting of net contents.

The incidence of major damage, compared between pot and trawl gears, large and small trawl vessels, and commercial trawlers and research trawler were analyzed by chi-square goodness of fit (Sokal and Rohlf 1969).

Delayed Mortality

Damaged and undamaged American lobsters less than the minimum length were taken from the same area of Long Island Sound, on the same date, from commercial pot vessels and from either commercial trawl vessels or research vessel. Samples were obtained in November 1983 and May, July, and August 1984. They were transported in tanks with circulating seawater to a laboratory equipped with an open circulating seawater system and were observed twice daily for a period of 14 days. Lobsters were fed daily with assorted fish species. Dead lobsters were removed upon observation. Lobsters were selected nonrandomly from catches to ensure that damaged lobsters were adequately represented in the tests. Since damaged lobsters often made up only a small percentage of the total, our sample consisted of proportionally more damaged lobsters than their actual proportion in the catch.

American lobsters with minor damage were combined with undamaged ones for analysis because undamaged lobsters rarely experienced delayed mortality (2/309) and those with minor damage never did. To estimate total delayed mortality from each gear, the observed delayed mortality rate in each test category (undamaged hardshell, damaged hardshell, and newshell) was extrapolated to the corresponding trawl catches of undamaged, damaged, and newshell lobsters observed during the same months in 1984. The laboratory mortality rate for newshell lobsters was applied to all newshell lobsters in commercial catches rather than only damaged newshell lobsters since internal (unobserved) damage may have occurred. Field data from 1984 commercial catches were used to estimate total trawl-induced mortality because the proportion of newshell lobsters in commercial catches was highest during 1984, and we believe that that year's data most accurately represent the proportion of newshell lobsters taken in the fishery.

The chi-square goodness of fit (Sokal and Rohlf 1969) with Yates' correction for continuity (Zar 1974) was utilized to determine whether lobster mortality rates differed between large and small trawl vessels and between commercial and research trawl vessels. The effect of season and molt condition was examined using a log-likelihood ratio test (G-test; Sokal and Rohlf 1969). Seasonal

changes were defined by water temperature variation whereas molt condition (newshell vs. hardshell) was based on the bimodal distribution of lobster molting (June-July and October-November) observed in Long Island Sound (Lund et al. 1973). The relationship between temperature and shell condition was evaluated by comparing data derived from postmolt periods following the summer (warming seawater temperature) vs. fall (cooling seawater temperature) molts. Postmolt lobsters recovered from the capture process in flowing seawater of 20°C in the July test and 15°-16°C in the November test. Intermolt lobsters in May recovered in 12°C seawater and, in August-September, at 22°C. In all cases, seawater temperatures reported here were elevated approximately 1°-2°C from passage through the circulation system.

The trawl-caught sample included 74 lobsters taken from research vessel catches. Comparison of delayed mortality rates between research and commercial samples revealed no significant difference ($\chi^2 = 0.305$) so the samples were pooled. Delayed mortality rates from samples taken from small (12 m) and large (20 m) trawl vessels in November 1983 and August 1984 were not significantly different ($\chi^2 = 0.05$), therefore, large and small vessel data were also pooled. All damage observations were recorded in the same manner as reported above.

Mortality Due to Freezing

Seventy hardshell, undamaged, trawl-caught American lobsters <81 mm CL were held in an open circulating seawater system at 8°C. On 15 January 1985, three groups of 20 lobsters were exposed in a wooden box (2 m × 1 m × 0.3 m) to ambient air temperature of −9.5°C for periods of 30, 60, and 120 minutes. The remaining 10 lobsters were held without exposure as a control. After the prescribed time had elapsed, the test lobsters were returned to the holding system and observed several times during the following 48-h period for incidence of mortality.

RESULTS

Incidence of Damage Due to Trawling

Damage to American lobsters of all sizes caused by commercial trawling throughout the 19-mo sampling period is summarized in Table 1. The monthly incidence of major damage (including immediate mortality) varied seasonally, from 0 to 14.0% in the trawl fishery and from 0 to 3.5% in the pot fishery. Minor damage ranged from 0.9 to 8.1% in the trawl fishery and from 0 to 10.7% in the pot fishery. Differences between pot and trawl damage rates were compared only for months in which both gears were sampled. The incidence of major damage was significantly greater for trawl samples in July and October-November, but not in August or September (Table 2).

The incidence of damage due to the two gears

TABLE 1.—Incidence of damage to American lobsters taken by commercial otter trawl from July 1983 through January 1985.[1]

Month		Major damage: Broken parts	Major damage: Multiple injuries	Major damage: Dead	No major damage: Minor damage	No major damage: Undamaged	Total (*n*)
Jan.	(*n*)	1	0	2	6	91	100
	(%)	1.0	0	2.0	6.0	91.0	
Feb.	(*n*)	0	0	0	1	14	15
	(%)	0	0	0	6.7	93.3	
Mar.	(*n*)	6	3	0	9	557	575
	(%)	1.0	0.5	0	1.6	96.9	
Apr.	(*n*)	19	8	4	25	1,461	1,517
	(%)	1.3	0.5	0.3	1.6	96.3	
May	(*n*)	22	7	0	21	1,087	1,137
	(%)	1.9	0.6	0	1.9	95.6	
June	(*n*)	1	1	4	2	216	224
	(%)	0.5	0.5	1.8	0.9	96.3	
July	(*n*)	72	44	16	57	854	1,043
	(%)	6.9	4.2	1.5	5.5	81.9	
Aug.	(*n*)	18	4	1	36	1,056	1,115
	(%)	1.6	0.4	0.1	3.2	94.7	
Sept.	(*n*)	49	4	23	36	1,242	1,354
	(%)	3.6	0.3	1.7	2.7	91.7	
Oct.	(*n*)	94	47	25	116	1,426	1,708
	(%)	5.5	2.7	1.5	6.8	83.5	
Nov.	(*n*)	133	128	50	181	1,738	2,230
	(%)	6.0	5.8	2.2	8.1	77.9	
Dec.	(*n*)	77	20	13	68	998	1,176
	(%)	6.5	1.7	1.1	5.8	84.9	

[1]Data from months in successive years are pooled.

TABLE 2.—Incidence of damage to American lobsters taken by commercial pot and otter trawl gears, 1983-84.

Month	Pot fishery: Major damage	Pot fishery: *N*	Trawl fishery: Major damage	Trawl fishery: *N*	χ^2
July	0.9%	2,165	12.7%	1,043	212.2**
August	1.3%	1,512	2.1%	1,115	1.8
September[1]	3.5%	424	5.9%	1,344	2.4
Oct.-Nov.[1]	0.6%	661	14.4%	2,672	96.8**

**significantly different ($P < 0.001$).
[1]1983 data only (no pot fishery samples taken in 1984).

was analyzed with respect to shell hardness and carapace length (<81 mm vs. ≥81 mm). Size-specific damage to newshell American lobsters taken in the trawl fishery was significant with smaller lobsters incurring more damage (43% vs. 30%, $\chi^2 = 6.64$, $P = 0.01$). There were no size-specific differences in damage to newshell lobsters taken in the pot fishery or to hard-shelled ones in either fishery.

Trawled egg-bearing female American lobsters (always hard shelled) incurred 1.9% major damage, no immediate mortality, and 2.1% minor damage throughout the sampling period ($n = 909$). Eggbearers ≥81 mm CL ($n = 585$) exhibited 2.2% major damage and 2.4% minor damage while those <81 mm CL ($n = 306$, 18 size unspecified) incurred 1.3% major damage and 1.6% minor damage. Pot-caught eggbearers sustained 0.9% major, and 0.8% minor damage throughout the sampling period ($n = 1,926$). One of 1,926 pot-caught egg-bearers (0.05%) died on deck. These data suggest that the damage and immediate mortality to gravid American lobsters associated with both fisheries is minimal.

From September 1983 through December 1984, trips were made with both large (15-26 m) and small (12-14 m) trawl vessels during eight different months. In two of those months, damage rates were equal, in two they differed by <1%, and in four they ranged from 7.3% higher for small vessels to 13.7% higher for large vessels. The difference exhibited in the four months for which deviations of more than 1% were observed was not significant ($\chi^2 = 0.019$, $P < 0.5$) indicating that damage to trawled American lobsters is independent of vessel size.

Trawl-induced damage occurred at similar rates in cold-water vs. warm-water intermolt periods (2.2% January-June vs. 3.1% August-September) and between cooling and warming postmolt periods (11.5% October-December vs. 12.6% July; Table 1). This suggests that damage due to trawling is more a function of shell condition than water temperature.

Delayed Mortality

From November 1983 to August 1984, 526

TABLE 3.—Estimated mortality to American lobsters <81 mm CL (delayed and immediate) due to otter trawling in 1984. Actual delayed mortality is computed by multiplying the percent occurrence of each damage category in trawl catches by the laboratory delayed mortality rate for that category. Total mortality rate is the sum of the actual delayed mortality plus immediate mortality observed on deck.

Month	Trawl catches %	Laboratory delayed mortality rate %	Actual delayed mortality %	Observed immediate mortality %	Total mortality rate %
May (N = 608, trawler catches; N = 41, laboratory samples)					
Hardshell					
undamaged	96.5	0	0	0	0
damaged	2.0	85.7	1.7	0	1.7
Newshell	1.5	33.3	0.5	0	0.5
			2.2	0	2.2
July (N = 533, trawler catches; N = 40, laboratory samples)					
Hardshell					
undamaged	81.8	10.5	8.6	0	8.6
damaged	9.9	85.7	8.5	2.1	10.6
Newshell	6.2	33.3	2.1	0	2.1
			19.2	2.1	21.3
August (N = 456, trawler catches; N = 146, laboratory samples)					
Hardshell					
undamaged	98.2	0	0	0	0
damaged	0.7	85.7	0.6	0	0.6
Newshell	1.1	33.3	0.4	0	0.4
			1.0	0	1.0
November (N = 408, trawler catches; N = 147, laboratory samples)					
Hardshell					
undamaged	86.3	0	0	0	0
damaged	3.9	42.4	1.7	1.2	2.9
Newshell	7.8	33.3	2.6	0.8	3.4
			4.3	2.0	6.3

American lobsters <81 mm CL, taken from pot and trawl vessels, were held to estimate trawl-induced delayed mortality (Table 3). Of 374 trawl-caught lobsters held in the laboratory, 47 (12.6%) had sustained major damage. Eighteen were newshell and were treated as one category regardless of damage sustained. Two of 309 (0.6%) undamaged, hardshell trawl-caught lobsters died whereas 55.3% of damaged ones died within the 14-d period, most within the first 7 days. Six of 18 newshell lobsters died (33.3%). Of 153 pot-caught lobsters, 8 (5.2%) had major damage; none were newshell. No pot-caught lobsters experienced delayed mortality.

Laboratory delayed mortality rates for damaged hardshell American lobsters were pooled in May, July, and August because of the small sample sizes ($n = 14$). Delayed mortality rates ranged from 50 to 100% in the three months. The mean (85.7%) was applied to the proportion of damaged hardshell lobsters in the commercial trawl fishery in each of those months. In November, a 42.4% delayed mortality rate ($n = 33$) was applied to the damaged lobster category in November commercial samples. Although only two undamaged hardshell lobsters died, both occurred in July (2 of 19). This proportion (10.5%) was applied to the proportion of undamaged hardshell lobsters in the July commercial catches. Since no delayed mortality occurred to undamaged hardshell lobsters in May, August, or November, no delayed mortality rate was applied to that category for those months. The delayed mortality rate for newshell lobsters (33.3%, $n = 18$) was applied to the proportion of newshell lobsters in commercial catches (1-8%). Immediate (on-deck) and delayed mortality rates for lobsters <81 mm CL and for each shell condition (undamaged hard, damaged hard, and newshell) were summed, resulting in an estimate of total mortality for each season (Table 3).

Estimated trawl-induced mortality rates for the four sample periods were tested to determine the relative importance of high seasonal water temperatures (July and August) and molting (November and July). November and July had significantly higher rates of mortality than May and August (Tables 3, 4), indicating that molt condition (July and November) is more important in determining the extent of mortality than water temperature. There was no significant difference between May and August delayed and immediate mortality estimates (Table 4) despite a 10°C difference in water temperature. However, warm temperatures appeared to increase the incidence of mortality after molting since the July rate was significantly higher than the November rate (21.3% vs. 6.3%, Table 4).

TABLE 4.—Log-likelihood ratio test of expected trawl-induced mortality to American lobsters <81 mm CL, by season. Underlining denotes no significant difference at $P = 0.05$. $\chi^2 = 178.4^*$ overall, 44.8^* (July-November), 11.8^* (November-May), and 1.8 (May-August).

	May	August	November	July
Water temperature	cold	warm	cold	warm
Molt condition	nonmolting		molting	
Estimated mortality	2.2%	1.0%	6.3%	21.3%

*= $P < 0.005$.

Mortality Due to Freezing

Exposing undamaged American lobsters to ambient air temperatures of −9.5°C produced no mortality at 30-min exposure, and 70% and 100% mortality at 60 minutes and 120 minutes, respectively. Damaged lobsters were not tested since they occur so infrequently during cold-water periods of the year (Table 1). Freezing temperatures may also induce reflex amputation (autotomy) of claws. One lobster of 20 in the 30-min sample and four American lobsters of 20 in the 60-min sample autotomized one claw.

DISCUSSION

Jamieson and Campbell (1985) found that sea scallop dragging in eastern Canada could damage American lobsters, but since the sea scallop and lobster fisheries generally were not simultaneous (lobsters tended to emigrate from the scalloping areas each season prior to the advent of the drag fishery), the use of scallop gear over beds that hold lobsters at other times posed no significant impact to the resource. Scarratt (1972) observed a similar situation in the eastern Canadian Irish moss rake fishery. Although American lobsters did suffer damage from the gear, most lobsters emigrated before the moss harvest season, so the damage associated with the gear was minimal. In western Long Island Sound, the lobster pot and mixed species trawl fisheries both operate throughout the year. Since the seabed in this area is relatively uniform and generally free of

obstructions to trawling, lobsters can be taken simultaneously with both gears, raising concerns that trawl gear is detrimental to the resource.

In Narragansett Bay, RI, using a 13 m stern trawl-rigged research vessel, Ganz (1980) found low immediate mortality to trawl-caught American lobsters and low damage rates during intermolt periods, and higher damage rates immediately following molting. He observed that hardshell lobsters were not likely to sustain critical injuries but postulated that commercial-scale operations might produce higher damage rates than the research vessel because of net compaction. We found that major damage (including immediate mortality) was greatest during molting periods, ranging from 12.6% in July to 14.0% in November. Hardshell (intermolt) lobsters suffered little damage by commercial trawling, with the monthly incidence of major damage and immediate mortality <3% from January through June and in August. Minor damage, including autotomy of claws, ranged from 0.9 to 8.1% and was greatest in October-November. Minor damage was <2% from March through June.

The incidence of immediate mortality by month never exceeded 0.5% in the pot fishery or 2.2% in the trawl fishery. Moreover, we found that damage rates were independent of vessel size, whether in the commercial fishery or between 12 m commercial and 13 m research vessels (see below). Newly molted American lobsters were damaged by both trawl and pot gears but trawling caused greater damage.

Spurr (1978) found experimental otter trawl-induced injury in summer to be greater in July than in September; however, since he aggregated minor damage with major damage and did not provide sample sizes, quantitative comparison of major damage between the two studies is not possible. Spurr concluded that lobster damage due to trawling in winter would be minor, a conclusion supported by our data.

Ganz (1980) suggested that damaged, sublegal American lobsters might suffer mortality upon release, although he did not investigate this possibility. We found that delayed mortality appeared to be influenced by the condition (incidence of damage) of American lobsters. Only 2 of 309 undamaged, hardshell lobsters experienced delayed mortality after trawling, compared to 26 of 47 (55.3%) damaged, hardshell, trawl-caught lobsters. Delayed mortality never occurred to lobsters with minor damage or autotomized claws. Although the sample size was small (n = 18), only one-third of all trawled newshell American lobsters experienced delayed mortality.

While both trawl and pot gear damage lobsters, trawl-caught lobsters alone sustained delayed mortality. One of the initial concerns about trawling was that visibly undamaged American lobsters less than the minimum length, returned to the water after trawling, would suffer a high level of unobserved mortality. Our results indicate that such mortality rarely occurs to undamaged American lobsters; consequently, potential delayed mortality may be ascertained simply by inspection of the incidence of major damage in the catch.

Of the two molting periods in Long Island Sound, a higher rate of mortality was observed in July than in November, possibly related to the warmer postmolt water temperatures which occur in summer compared with late fall. Damage rates during postmolt periods were similar (12.6% July vs. 14.0% November) notwithstanding the difference in water temperature. These results suggest that the resistance of trawled postmolt American lobsters may be lowered by warm seawater temperatures and that such temperatures may increase the occurrence of delayed mortality independent of the incidence of damage. Mean values of immediate and delayed mortality for all samples taken during intermolt periods were negligible (<1.0% and <2.0%, respectively).

There appeared to be some variability in mortality depending on the type of damage sustained. Damage to the abdomen and carapace was almost always lethal (100% and 92%, respectively), while broken parts such as claws or rostrum resulted in 25% and 50% mortality, respectively. However, small sample sizes precluded definitive analysis.

Ganz (1980) speculated that the most significant impact of trawling might be related to the cumulative effect of trawling and damaging sublegal American lobsters, and subsequently releasing them to be taken again. In discussing this possibility, he reported an immediate claw loss (cull) rate of 3.5% and a prior cull rate of 8.8%. This is a valid concern, and one which should be considered in both trawl and pot fisheries. For example, Smith (1977) reported a cull rate of 26% in an area of Long Island Sound which had not been trawled during recent years and a rate of 23% in an area lightly fished with trawls, suggesting that a high cull rate can occur in the absence of trawling (both areas were heavily fished with pots). These observations, while higher than Ganz's, included both new and old claw loss as well as lobsters with regenerated claws. In the

present study, minor damage (which included immediate claw loss) ranged from 0.9 to 8.1% per month in the trawl fishery and from 0 to 10.7% in the pot fishery.

While the mortality of trawled newshell American lobsters was high during the two molting periods, they represented such a small percentage of the total trawl catch (1-8%) that the estimated total mortality to the entire catch was little changed by their presence. Similarly, while damaged lobsters sustain a high rate of mortality, it is their proportion in the catch which determines the rate of additional mortality experienced by the population.

No truly soft American lobsters (stage A, after Passano 1960) were observed in the pot catches sampled for delayed mortality estimates, and they occurred rarely in other commercial pot samples (up to 3% in July 1984). They were observed infrequently in trawl catches as well (up to 7.8% in November 1984). The low incidence of soft lobsters in commercial catches is probably due to reduced mobility during the shell hardening process (Herrick 1909) when American lobsters are most vulnerable to damage and predation.

No significant difference was observed in damage rates or delayed mortality based on sampling of vessels <15 m or >15 m. There was no difference in delayed mortality rate between 13 m research vessel samples and either 12 m commercial or 15-26 m commercial trawlers. Finally, there was no difference between damage rates to American lobsters ≥81 mm CL taken by research and commercial vessels in October-November 1984, the only period for which comparable data (tows of 2-h duration) were available for both vessel categories. The former results suggest that trawl-induced damage and mortality is independent of vessel size; the latter suggests that observations of fishery-induced damage made by biologists were representative of actual fishing conditions.

While American lobsters may succumb to subfreezing air temperatures, consideration of this source of mortality is a function of both temperature and exposure time and must be judged on the behavior of the fishery in question. Edwards and Bennett (1980) reported a survival rate of 42-85% for *Nephrops norvegicus* after 1-h exposure to air, noting that favorable weather conditions and the type of vessel used were factors contributing to higher survival. In the present study, American lobsters exposed to −9.5°C air temperatures for 30 minutes all survived. Those exposed for 120 minutes all succumbed. Intermediate exposure (60 minutes) produced intermediate results (30% survival). In Long Island Sound, field observations during a 19-mo period suggested that operators in the trawl fishery commonly sorted the catch within 15-45 minutes.

Our design tended to maximize the debilitating effect of freezing temperatures. Trawl net contents are commonly released onto the vessel deck in a pile. Consequently, organisms on the inside of the pile are protected from cold air temperatures. In our test, all American lobsters were placed on a flat table with 0.3 m high sides; thus, all lobsters were equally exposed to freezing temperatures and none were able to benefit from the "piling" of a normal catch. As a consequence, this experiment very likely overstated the impact of subfreezing air temperatures on commercially taken American lobsters.

An additional consideration beyond the directed fishery is the mortality to "sublegal" American lobsters (those <81 mm CL) and the damage to lobsters during molting periods which may result from a mixed species trawl fishery which includes a so-called incidental catch or "bycatch" of lobsters. As with freeze-induced mortality, this factor must be judged based on the performance of the fishery in question.

In Connecticut, trawlers reported <10% of the commercial American lobster landings reported by all fishermen during the period 1982-86 (CT DEP fn. 2). However, given the controversy surrounding trawling during this investigation and the weaknesses inherent in catch reporting systems during periods of controversy (Matlock 1986; Ferguson 1986), a number of independent methods of observation were used to determine the actual impact to the resource associated with trawling. Unannounced boardings by Connecticut Conservation Officers were utilized to estimate the true magnitude of lobster catches. Biologists made sampling trips on the vessels of commercial trawl fishermen fishing in Long Island Sound to document the fishery-induced incidence of damage. Research vessel sampling was used to estimate a fishery-independent rate of trawl-induced damage. The results of these observations suggested that the magnitude of American lobster catches per trip was about the same as those reported in mandatory logbooks and, except during molting periods, trawl-induced damage was minimal.

Observations in controlled laboratory conditions were utilized to estimate the delayed

mortality which might be expected to occur to sublegal American lobsters returned to the water after trawling. These observations indicated that this source of mortality should only be a concern during molting periods. Since delayed mortality to sublegal American lobsters occurs to a significant degree only during molting periods, an incidental limit of some number of lobsters per day for trawlers during those periods represents an effective means to deter the directed fishery and protect sublegal American lobsters while allowing the finfish fishery to continue.

There has been considerable controversy in New England regarding the effects of trawling on the American lobster resource. This study provides three results of assistance to fishery managers dealing with this question. First, both pot and trawl gear damaged American lobsters, but trawl-induced damage occurred more frequently, and particularly during molting periods. However, damage was not always lethal and visibly undamaged lobsters virtually never sustained delayed mortality. Second, during molting periods, mortality caused by trawling reached 6-21%, depending on season. Delayed mortality was influenced most by the degree of damage sustained by the lobster. Therefore, while delayed mortality may be of considerable consequence to the resource during molting periods, it can be estimated by inspection of the condition of lobsters in the catch. Third, during intermolt periods, both immediate and delayed mortality due to trawling occurred infrequently (<1% and <2%, respectively). All these factors should be evaluated within the context of the biological and socioeconomic considerations inherent in the fishery management process.

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FACTORS AFFECTING COOKED TEXTURE QUALITY OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*, FILLETS WITH PARTICULAR EMPHASIS ON THE EFFECTS OF INFECTION BY THE MYXOSPOREANS *KUDOA PANIFORMIS* AND *K. THYRSITIS*

GEORGE KUDO, HAROLD J. BARNETT, AND RICHARD W. NELSON[1]

ABSTRACT

Pacific whiting is known to have abnormal cooked texture induced by enzymes of the Myxosporean parasites *Kudoa*. An extensive United States-Canadian joint research project was initiated to explore the correlation between texture quality and intensity of *Kudoa* infection. Enumeration of white and black pseudocysts and identification of the *Kudoa* species present was done by the Canadian team while texture quality was determined by the U.S. team. Data analysis showed that 1) white pseudocysts were more closely correlated with cooked texture quality than were black pseudocysts; 2) *K. paniformis* and mixed infections correlated well with sensory texture while *K. thyrsitis* infections correlated poorly; 3) Pacific whiting from southern fishing areas had higher white pseudocyst counts of *K. paniformis* and more soft abnormal texture than Pacific whiting from northern fishing areas; 4) nape and dorsal areas of fish had higher intensities of *Kudoa* infections and greater incidences of abnormal texture; 5) body length correlated weakly with texture quality, but there was no relationship between sex and sensory texture. Results of experimental evaluations indicate that the visual culling method may have some potential for use in sorting Pacific whiting with white and/or black pseudocysts. However, the white pseudocysts require careful examination to be detected. Therefore, a visual culling method may be too time consuming to be practical for use on a production line.

Between 1982 and 1984, the annual catch of Pacific whiting[2], also known as Pacific hake, *Merluccius productus*, harvested by American and foreign fishing fleets in the territorial waters off the Pacific coast of the United States, ranged between 80,000 and 100,000 t. Of this amount, between 67,000 and 79,000 t were annually harvested by a joint venture fishery with the Soviet Union. The catch by other foreign countries, mainly Poland and Bulgaria, operating in the directed fisheries, ranged from 7,000 to 14,000 t[3]. Although the Pacific whiting resource has been estimated to vary between 445,000 and 3,440,000 t (Dark 1985), its domestic use has been limited because of soft texture associated with the presence of a parasitic Myxosporea of the genus *Kudoa*. Patashnik et al. (1982) and Tsuyuki et al. (1982) established that the flesh deterioration of infected Pacific whiting was due to an enzyme-induced proteolysis. However, the correlation between the degree of infection and the condition of the flesh was not entirely clear. Sometimes Pacific whiting heavily infected with the protozoan parasite appeared, when cooked, not to be affected, i.e., soft-textured, while lightly infected fish had very poor textures. The discovery by Kabata and Whitaker (1981) that Pacific whiting is infected by two different species of *Kudoa* (Fig. 1) explained some of these discrepancies. Tsuyuki et al. (1982) found that these species, *Kudoa paniformis* (Kabata and Whitaker 1981) and *Kudoa thyrsitis* (Gilchrist 1924), differ from each other in their enzyme activity, i.e., enzyme-induced proteolysis. Because Pacific whiting can be infected with one or both species of *Kudoa*, the final condition of the flesh might be determined by the type of *Kudoa* since *K. paniformis* is capable of producing much heavier infections than *K. thyrsitis* (Kabata and Whitaker 1981).

From a public health standpoint, no protozoan diseases of fish have been known to have man as host (Oppenheimer 1962) and myxosporea per se have never been reported to cause illness in humans (Konagaya 1982; Nagahisa et al. 1983). Nonetheless, infection with *Kudoa* continues to

[1]Utilization Research Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]The U.S. Food and Drug Administration has ruled that this species can be marketed as Pacific whiting (Robins et al. 1980).

[3]W. Daspit, OFIS, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115, pers. commun. March 1985.

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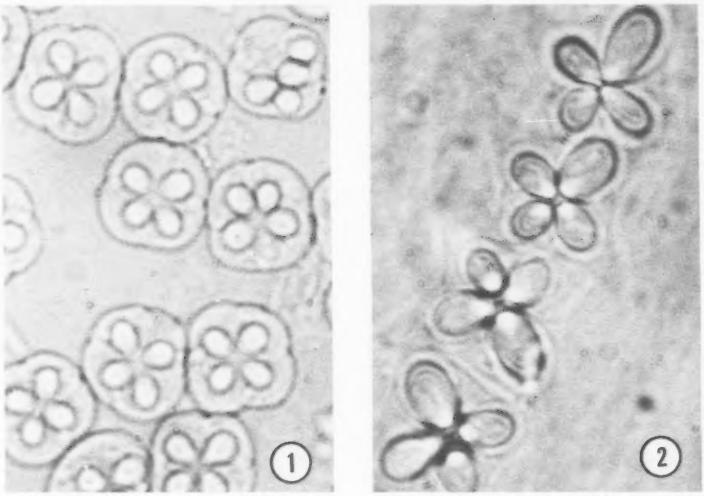

FIGURE 1.—Unstained spores at ×2400, (1) *Kudoa paniformis* (approximately 8 μm in size) and (2) *Kudoa thyrsitis* (about 15 μm in size), found in the muscle of Pacific whiting. *Photo by Carla Stehr.*

be a serious limiting factor in the Pacific whiting fishery.

A joint U.S.-Canadian project aimed at taking the full measure of these problems was initiated in 1983. The purpose of this paper is to report on the results of investigations into cooked flesh texture and its relationship to the intensity and type of *Kudoa* infection. The paper also correlates subjective sensory texture values with objective instrumental readings and establishes texture quality profiles of fish taken in different geographic areas along the distribution range of the Pacific whiting. Other factors, such as sex, body size, and location of infection within the various parts of the fish (i.e., anterior, posterior, dorsal, ventral) which might influence texture quality, were also examined. Finally, visual culling was evaluated to determine if sorting Pacific whiting infected with pseudocysts from the pack was practical.

MATERIALS AND METHODS

The sample used in this investigation consisted of 579 Pacific whiting collected by National Marine Fisheries Service personnel aboard the chartered MV *Nordfjord* in 37 hauls off the Pacific coast of North America, between lat. 37°18′N (near San Francisco) and 48°54′N (west coast of Vancouver Island) in the four International North Pacific Fisheries Commission (INPFC) areas (Fig. 2). The fish were caught between 16 July and 28 September 1983, in 30-min tows at depths ranging from 34 to 164 fathoms. Water temperatures at the cod end ranged between 7.5° and 10.5°C, while surface temperature ranged between 12.1° and 18.8°C. These temperatures were somewhat warmer than those in previous years, due to the 1982-83 El Niño effect (Weinberg et al. 1984). The Pacific whiting catch varied from 7 to 2,053 kg in the total catch of 20 to 2,488 kg per haul (Weinberg et al. 1984). A 32 mm (1 1/4″) stretched mesh size cod end liner was used to retain small fish. Each fish was measured and sexed, individually numbered, and frozen aboard the vessel. The fish samples were taken to the Utilization Research Division (URD) laboratory of the Northwest and Alaska Fisheries Center (NWAFC) in Seattle where they were sectioned longitudinally and each half labeled accordingly. One half of each fish was shipped to the Pacific Biological Station in Nanaimo, B.C., Canada, for parasitological examination, and the other retained by the URD laboratory for determination of flesh quality.

The parasitological methods used by the Pacific Biological Station are described elsewhere (Kabata and Whitaker 1986). Intensity of infec-

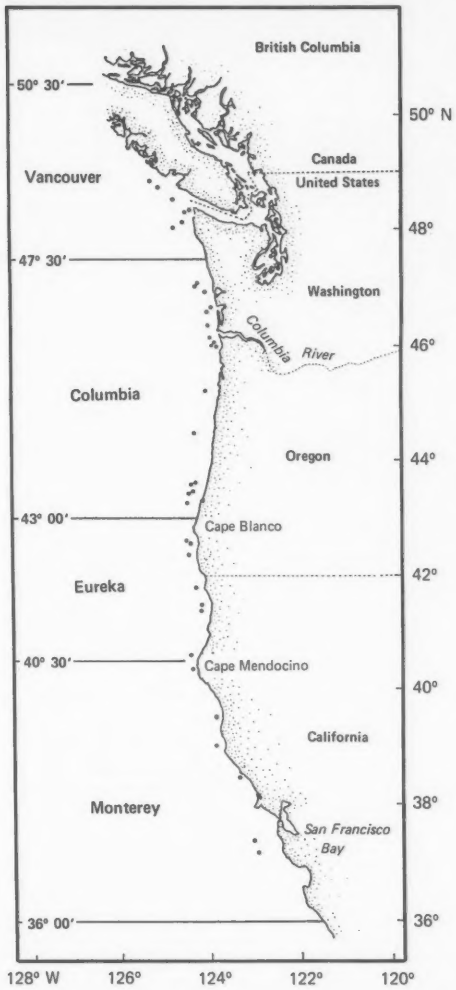

FIGURE 2.—Locations of the 37 hauls (black dots) of Pacific whiting made by MV *Nordfjord* and the International North Pacific Fisheries Commission (INPFC) areas surveyed in the summer of 1983.

tion with *Kudoa* was measured in each fillet, which were divided into six inspection areas (Fig. 3) as numbers of pseudocysts (i.e., infected muscle fibers) per gram of tissue. Separate counts were taken for each species of *Kudoa* and for white (young) and black (old) pseudocysts.

The flesh texture was determined in two ways: 1) by a sensory technique developed especially for Pacific whiting and 2) by mechanical shear press. The sensory texture evaluations were made by two project personnel experienced with Pacific whiting texture. Normal taste panel methods could not be used in this study because each sample fillet was divided into six areas for sequential evaluation, similar to the method described by Patashnik et al. (1982). The project personnel used a combination of taste and touch techniques to determine hardness sensation. The touch technique consisted of estimating hardness or resistance by pressing on the sample with the tip of the index finger. Taste texture was determined by the subjective force required to bite through the sample with the molar teeth.

Texture ratings were based on a 9-point hedonic scale (Table 1) where scores of 9 to 5 described normal textures ranging from the firmness of rockfish to the tenderness of typical Pacific whiting, 4 to 3 as the softness of sole, and 2 to 1 as an abnormal or mushy to liquefied texture.

Prior to measuring sensory textures, the frozen Pacific whiting halves were placed on racks in trays, tempered at ambient temperature for approximately 2 hours or until semifrozen, covered with aluminum foil, and then, depending on the

TABLE 1.—Sensory texture category based on a 9-point hedonic scale.

Category	Scale	Description
Normal	9	Very firm and flaky as in rockfish
	8	Very firm and flaky as in rockfish
	7	Firm and flaky as in true cod
	6	Tender and slightly flaky as in typical Pacific whiting
	5	Tender and slightly flaky as in typical Pacific whiting
Soft	4	Soft as in sole and flounder
	3	Soft as in sole and flounder
Abnormally soft[1]	2	Mushy
	1	Liquefied

[1]Considered organoleptically unacceptable as previously described by Patashnik et al. (1982) and Nelson et al. (1985).

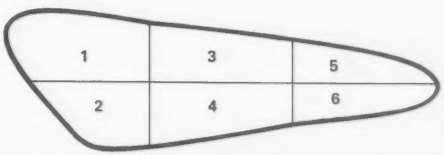

FIGURE 3.—Selected Pacific whiting fillet areas examined for cooked texture and pseudocyst intensity.

thickness, cooked in an oven at 375°F for 20 to 50 minutes. The texture of the fish was then determined organoleptically.

Mechanical texture was determined on 180 randomly selected fish, in which duplicate shear press readings were taken on 15 g of muscle tissue removed from the dorsal portions of the fish samples to correlate with the portions taken for sensory evaluations. The successful use of mechanical texture analysis to correlate with the sensory texture of Pacific whiting was previously reported by Nelson et al. (1985). The tissues were teased into flakes which were leveled to a height of 8 mm in a Kramer shear-compression cell which was reduced in size to 29 mm wide, 71 mm long, and 64 mm deep to accommodate the sample. The assembly, consisting of four blades, was similar to the one described by Bilinski et al. (1977) and used by Tsuyuki et al. (1982) to evaluate objectively the texture of Pacific whiting. The cell operated in conjunction with the Food Technology Corporation FTA 3000 transducer[4], TP-4 Texturepress, and the TR-5 Texturecorder. A plot was made of the force required to drive the blades through the sample at a ram speed of 1 cm per minute and at a set recorder range. The peak force in pounds per 15 g tissue was calculated from the plot (Bourne 1982).

Culling was performed on partially thawed halves of fish. Pseudocysts are visible as white or black threads of varying intensities imbedded longitudinally along the muscle fibers. The culling categories were modeled after the scheme of Patashnik et al. (1982) for both white and black pseudocysts as none, light (<20%), moderate (20 to 30%), and heavy (>30%) as determined visually, based on the percent area of fillet affected.

Only fish over 27 cm were used for all analyses, since in commercial operations fish smaller than 27 cm would not likely be taken because domestic and foreign fishermen use 50 mm (2 in) to 100 mm (4 in) cod end mesh size as regulated by the Pacific Coast Groundfish Fishery Management Plan.[5]

Data representing sensory textures and *Kudoa* pseudocyst counts (made on a total of 562 fish exclusive of fish under 27 cm) were analyzed on the NWAFC Burroughs 7800 computer system using the SPSS software package described by Nie et al. (1970) and SPSS Update 7-9 (Hull and Nie 1981).

Fitted regression curves between cooked texture values and white and black pseudocyst counts were drawn using robust locally weighted regression analyses described by Cleveland (1979). The method was used to smooth scatterplots by calculating a polynomial fit to data using weighted least squares.

RESULTS AND DISCUSSION

Relationship Between Sensory Texture Ratings and Shear Press Values

Since any nonsensory evaluations of a fishery product must ultimately relate to the products' intrinsic organoleptic properties, emphasis in this study was placed upon taste tests despite the inherent fatigue factor associated with testing large numbers of samples. No consumer-type panel was carried out to test the accuracy of the texture evaluation, because fish with abnormal

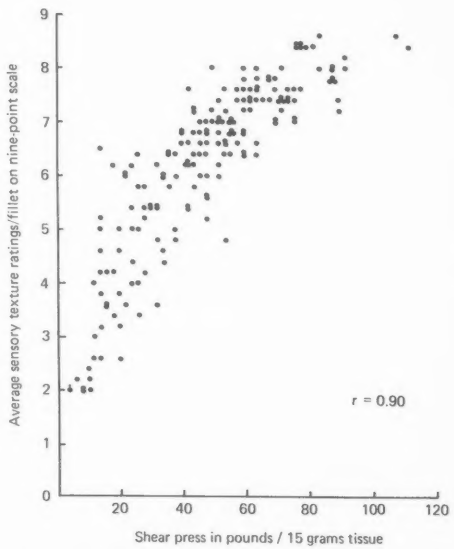

FIGURE 4.—Scatterplot and Spearman correlation coefficient (r) between sensory texture rating and shear press force of cooked flesh of Pacific whiting fillets.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]J. Wall, REFM Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115, pers. commun. March 1985.

texture were purposely included in the present study to determine the extent of the problem. On randomly selected samples, shear press measurements were run concurrently as an objective support for the sensory data.

A scatterplot and the Spearman correlation coefficient (nonparametric) determined for the sensory texture ratings and shear press values shown in Figure 4 was produced by the SPSS software. The high degree of correlation ($r = 0.90$ at $P = 0.001$) was found to support the credibility of sensory texture evaluation in this study.

Effect of White and Black Pseudocysts and *Kudoa* Species Upon Sensory Texture

Fitted regression curves for sensory texture values and white pseudocyst counts are shown in Figure 5A. Mixed infections include both *K. paniformis* and *K. thyrsitis* pseudocysts in the same fish. The curve representing the white mixed infection shown superimposed on that of the white *K. paniformis* curve suggests that most of the white mixed pseudocysts consisted of *K. pani-*

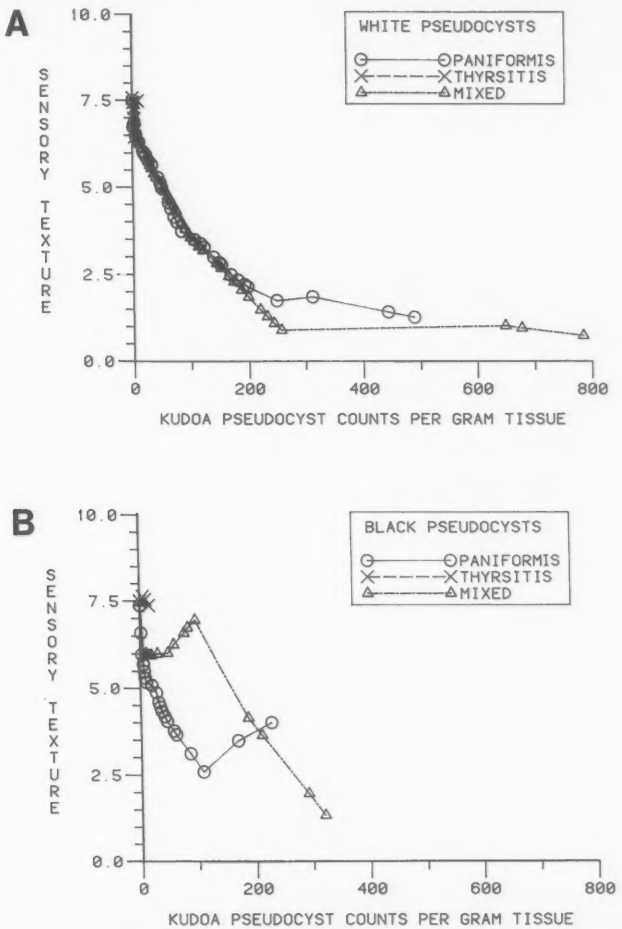

FIGURE 5.—Fitted regression curves between cooked texture of Pacific whiting and intensity of (A) white *Kudoa* pseudocysts and (B) black pseudocysts.

formis. Correlation values for these two curves were $r = -0.79$ and -0.80, respectively (Table 2). Pseudocyst counts of white *K. thyrsitis* were <10 and did not appear to adversely affect the texture of the Pacific whiting (Table 3A). The low count is thought by Kabata and Whitaker (1981) to be the result of an evolutionary development of defense mechanisms in the host fish. The correlation coefficient representing sensory textures and white *K. thyrsitis* infection was 0.12. This suggests that *K. thyrsitis* plays an insignificant role in the texture quality of Pacific whiting, a view also held by Kabata and Whitaker (1981).

Fitted regression curves between sensory textures and black pseudocyst counts are shown in Figure 5B. Mixed black pseudocyst counts did not follow the pattern for black *K. paniformis* counts, as observed with the white mixed and *K. paniformis* infections. This suggests that the black pseudocyst counts cannot be used as a reliable predictor of sensory texture. Magnitudes of black *K. paniformis* counts and black mixed counts were <320, while counts were <16 for black *K. thyrsitis*. Like those infected with white *K. thyrsitis*, fish infected with black *K. thyrsitis* parasites had normal, firm cooked textures (Table 3A). The absolute value of the Spearman correlation coefficient (Table 2) between texture quality and black pseudocyst intensity was lower (−0.38) than that of the coefficient for texture quality and white pseudocyst intensity (−0.74), both at significance level of 0.001.

From the correlation coefficients for the white and black pseudocyst counts of both species, the square of the coefficients (coefficient of determination) was calculated to compare their relative importance in terms of differences in their magnitude with respect to one another. Fifty-five percent of the observed variability in all sensory texture ratings can be accounted for (predicted) by the observed variability in the white pseudocyst counts, while only 14% can be accounted for by the observed variability in the black pseudocysts counts. However, infections do not occur in Pacific whiting as only white or black pseudocysts; they also occur as a mixture of the two. Thus, when the quantitative effects of the white or black pseudocyst counts on sensory texture were evaluated by multiple regression analysis, we found that only 1.5% of the variability in sensory texture rating was accounted for by black pseudocyst counts, and 45% accounted for by white pseudocyst counts. These figures represent partial coefficients of determination which indicate the relationship between two variables while controlling the effects of one or more other variables and are consistent with the findings of Patashnik et al. (1982) and Tsuyuki et al. (1982).

TABLE 2.—Spearman correlation coefficient between sensory texture rating and *Kudoa* pseudocysts in Pacific whiting caught during the summer of 1983.

Sensory texture with:	Sample size	Correlation coefficient	Significance
White pseudocysts			
total population	562	−0.74	0.001
Black pseudocysts			
total population	562	−0.38	0.001
K. paniformis			
white pseudocysts	201	−0.80	0.001
black pseudocysts	201	−0.66	0.001
K. thyrsitis			
white pseudocysts	191	−0.12	0.05
black pseudocysts	191	0.07	0.15
Mixed infection			
white pseudocysts	259	−0.79	0.001
black pseudocysts	259	−0.49	0.001

TABLE 3.—Percentage of sensory texture ratings for (A) each *Kudoa* species, (B) fork length, and (C) sex composition for Pacific whiting caught during the summer of 1983.

Description	Sample size	Sensory texture rating (%)			
		Normal	Soft	Abnormal	Total
(A) *Kudoa* species					
K. paniformis	144	17	5	3	26
K. thyrsitis	125	22	0	0	22
Mixed infection	190	23	7	4	34
None	103	18	0	0	18
Total	562	80	12	7	100
(B) Fork length composition of whiting					
Small (27-39 cm)	144	93	5	2	100
Medium (40-49 cm)	172	79	17	4	100
Medium large (50-59 cm)	170	74	14	12	100
Large (60-80 cm)	76	72	15	13	100
All lengths	562	80	13	7	100
(C) Sex composition of whiting					
Female	332	81	12	6	100
Male	227	79	13	8	100
Total	559	80	13	7	100

Intensity of White and Black Pseudocyst Infection in Relation to Sensory Texture Ratings

The magnitude of white and black pseudocyst counts in relation to their corresponding sensory texture scores are shown in Tables 4 and 5.

A total of 214 fish, 38% of the fish examined, did not have white pseudocysts. Table 4 shows that texture scores for this group of fish range from 4 to 9 with 97% of the scores in the range of

6 to 8. Fish infected with white pseudocysts to the degree of 26 to 50 counts (average for the six areas in each fish tested) resulted in 1 out of 50 fish tested with a sensory texture score of 2. Thus, 2% of the fish in this category must be regarded as too soft and are organoleptically unacceptable (Table 1). In the sample of 562 fish, 25 specimens were found with white pseudocyst counts ranging between 51 and 75, none of which were judged to have a texture score of 2 or lower. However, note that 11 of 25 (44%) fish samples were soft textured. When the white pseudocyst counts were 76 or higher, nearly all of the fish were soft or abnormally soft textured.

The frequency distribution of sensory texture scores vs. black pseudocyst counts (Table 5) does not show the same relationship that intensity of white pseudocyst infection had on sensory texture (Table 4). This becomes evident after examining sensory texture scores for fish with black pseudocyst counts of 1 to 25 (Table 5) when the entire range of texture scores is represented.

Note, however, that the observed distributions of white and black pseudocysts differ. For example, of the 98 fish with pseudocyst counts exceeding 50, 81 had white pseudocysts but only 17 had black pseudocysts. Also, for Pacific whiting with counts >100, 37 of 45 (82%) with white pseudo-

TABLE 4.—Frequency distribution of fish in each sensory texture score category and intensity of white pseudocyst infection in Pacific whiting over 27 cm. $n = 562$.

White pseudocyst count (ave./fillet)	Number of fish in each sensory texture score category									Row total	Percent of n
	9	8	7	6	5	4	3	2	1		
0	5	131	69	7	1	1				214	38.1
1-10	2	49	59	24	14	2	1			151	26.9
11-25	1	5	15	23	11	9	2			66	11.7
26-50		3	5	18	14	5	4	1		50	8.9
51-75			2	3	9	10	1	0		25	4.4
76-100			0	1	2	3	3	0	2	11	2.0
101-125		1	0	1	1	1	4	5	1	14	2.5
126-150						1	1	1	0	3	0.5
151-200						2	3	9	2	16	2.8
201-300							1	1	4	6	1.1
301-400						1	0	0	0	1	0.2
401-800								1	4	5	0.9
Total of infected fish	3	58	81	70	51	34	20	18	13	348	
Percent of n	0.5	10.3	14.4	12.5	9.1	6.0	3.6	3.2	2.3	61.9	100.0

TABLE 5.—Frequency distribution of fish in each sensory texture score category and intensity of black pseudocyst infection in Pacific whiting over 27 cm. $n = 562$.

Black pseudocyst count (ave./fillet)	Number of fish in each sensory texture score category									Row total	Percent of n
	9	8	7	6	5	4	3	2	1		
0	2	97	72	15	9	4	3	2	0	204	36.3
1-10	5	74	62	42	31	21	8	6	4	253	45.0
11-25	1	14	10	9	8	5	4	5	2	58	10.3
26-50		4	3	7	4	4	1	4	3	30	5.3
51-75			1	2	0	0	2	0	0	5	0.9
76-100			2	0	0	0	1	0	1	4	0.7
101-125					0	1	0	0	1	2	0.4
126-150					0	0	0	0	0	0	0
151-200				1	0	0	0	0	1	2	0.4
201-300				1	0	0	1	1	0	3	0.5
301-400									1	1	0.2
401-800										0	0
Total of infected fish	6	92	78	62	43	31	17	16	13	358	
Percent of n	1.1	16.4	13.9	11.0	7.7	5.5	3.0	2.8	2.3	63.7	100.0

cyst counts and 5 of 8 (63%) with black pseudocyst counts fell in the 1 to 3 texture category. Although the data are limited, this may suggest that for lower counts black pseudocysts are not related to poor texture, whereas for higher counts, they are ($r = -0.38$ at $P = 0.001$).

In this study, 459 out of 562 fish were infected with the myxosporean parasite *Kudoa*. However, knowing that only white pseudocysts contain the parasites that produce the proteolytic enzymes that adversely affect texture (Tsuyuki et al. 1982), the assessment of the effect of pseudocyst infections on texture was necessarily confined to white pseudocyst counts only. Therefore, in order to determine the most likely white pseudocyst count which, when exceeded, would produce an abnormal texture in the cooked fish, the following analysis was made. On the scale of firmness in Table 1, the minimum acceptable texture value was defined as 3. Only 20 fish were rated 3. Their mean intensity of infection was 94.9 pseudocyst counts and median intensity was 88. Consequently, fish with median intensity ≥88 pseudocyst counts were hypothesized to be abnormally textured. On a qualitative scale this level of infection was considered heavy. To test this hypothesis, all fish having infection intensities ≥88 white pseudocyst counts were computer selected. There were 50 such fish. These included 90.3% of all the fish with abnormal textures (sensory rating of 1 to 2), but also included 3.9% of all the normal or soft-textured fish (sensory rating of 3 to 9). Next, fish with average sensory textures (5) were selected to determine the white pseudocyst counts below which sensory textures would most likely be normal. The median pseudocyst count for these fish was 23. Counts below 23 were considered indications of a light infection. The level of infection between these two counts (23 to 88) was considered to be moderate.

Because black pseudocyst counts correlated poorly with sensory texture in this study, the degree of black pseudocyst infection had to be arrived at from cullability figures using the culling techniques described previously. The cullability categories were determined visually and, like the white pseudocysts, described as light, moderate, and heavy. Confidence limits for black pseudocyst counts for each cullability category were statistically determined and the midpoint between the high end of one confidence limit and the low end of the adjoining confidence limits was taken as the dividing point. The following range of black pseudocyst counts was arrived at for each category: none (0); light (1 to 28); moderate (29 to 79); heavy (80 or more).

Effect of Geographical Areas

Data in Figure 6A shows the percentage of the catch from the various survey areas sampled in this study and their related sensory textures. Based on results of our sensory evaluations, 13% of the Pacific whiting harvested from the Monterey-Eureka, CA, sampling areas had abnormal textures, whereas only 1 to 3% of the Pacific whiting caught between the Columbia River and Vancouver Island had abnormal textures. The correlation coefficient between survey area and sensory texture rating was 0.20 at $P = 0.001$.

Similarly, the incidence of heavy white pseudocyst infection (>88 pseudocyst counts) was about threefold greater in the Pacific whiting from the Monterey-Eureka, CA, corridor (Fig. 6B) than in whiting caught between the Columbia River and Vancouver Island, i.e., 16 to 11% vs. 5 to 4%. The percentage of no white pseudocyst found in the fish samples from all survey areas ranged from 25 to 34%.

The trend in black pseudocyst counts (Fig. 6C) was similar to the trend in white pseudocyst counts in that more heavy (>80) black pseudocyst counts were observed in Pacific whiting caught between Monterey-Eureka, CA, and the Columbia River than in Pacific whiting from the Vancouver Island area. Two to three percent of the Pacific whiting sampled from the area between Monterey, CA, and the Columbia River were heavily infected with black pseudocysts, whereas no heavy black pseudocyst infections were found in the Pacific whiting caught from Vancouver Island area. Infections of black pseudocysts in Pacific whiting from the Vancouver Island area were primarily light (1 to 29), the category into which 84% of the infected fish fell, and moderate infections (29 to 79), the category in which 4% of the infected fish fell.

Table 6A shows the prevalence of the *Kudoa* species found in Pacific whiting caught between Monterey, CA, and Vancouver Island, Canada. *Kudoa paniformis* was the predominant species (average 36 to 37%) found in the Pacific whiting taken in the Monterey-Eureka area, whereas *K. thyrsitis* was the predominant species (29 to 40%) in the fish caught north of the Columbia River. Mixed infections averaged 34% for the combined survey areas.

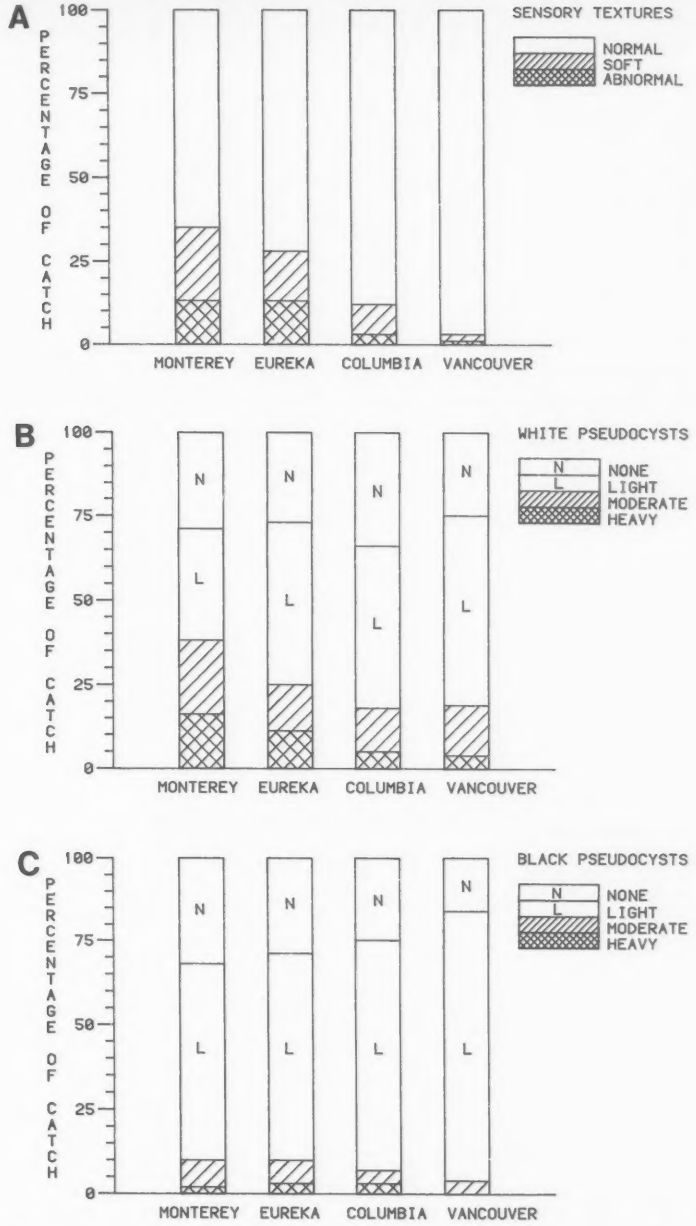

FIGURE 6.—Occurrence (%) of (A) sensory texture categories, (B) degree of white pseudocyst infection, and (C) degree of black pseudocyst infection of Pacific whiting, by INFPC areas.

TABLE 6.—(A) Prevalence of *Kudoa* species, (B) fork length composition (%), and (C) sex ratio of Pacific whiting samples in the INPFC catch survey area.

Description	INPFC survey area				
	Monterey	Eureka	Columbia	Vancouver	All areas
Sample size (fishes)	136	117	234	75	562
(A) *Kudoa* species (%)					
K. paniformis	36	37	18	15	26
K. thyrsitis	7	15	29	40	22
Mixed infection	35	27	35	39	34
None	22	21	19	7	18
(B) Fork length composition (%)					
Small (27-39 cm)	30	33	26	7	26
Medium (40-49 cm)	31	29	31	32	31
Medium large (50-59 cm)	27	28	30	40	30
Large (60-80 cm)	13	10	13	21	14
(C) Ratio of female/male	1.2	1.3	1.6	2.2	1.5

Effect of Biological Factors on Sensory Texture

Biological data showing sex composition, the ratio of females to males, and representative fork lengths (FL) and their relationship to corresponding sensory textures and survey areas are given in Tables 3B, 3C, 6B, and 6C, respectively. The ratio of females to males nearly doubled as fishing activities in this study moved from south to north along the Pacific coast. Concurrently, the fork length of the fish increased as well. About 60% of the largest fish (60 to 80 cm FL) were caught between the Columbia River and Vancouver Island. More abnormal textures were oberved in the larger fish than in the smaller fish (Table 3B). Based on the total number of specimens examined, however, the correlation coefficient for the relationship between fork length and sensory texture was low ($r = -0.21$ at $P = 0.001$).

Sensory texture was not found to be related to the sex of the fish ($r = 0.04$ at $P = 0.181$, Table 3C). The percentage of abnormal textures in the female and male fish was about the same, i.e., 6 and 8%, respectively, confirming the reports of Kabata and Whitaker (1981). Similarly, males and females were evenly distributed (approximately 12%) in the soft-texture category.

The Relationship of Pseudocyst Counts to Location of Infection in a Fillet Area to Texture

Results of analyses to determine the relationship of intensity of infection in a fillet area (Fig. 3) to texture quality are shown in Table 7. Pseudocyst infections were found throughout the fillet areas. The highest percentage (11 to 12%) of heavy infections of white pseudocysts were located in the nape area, whereas the lowest incidence (8%) was located in the tail ($r = 0.89$ at

TABLE 7.—Percentage of degree of *Kudoa* pseudocyst infection and corresponding sensory textures found in preselected examination areas of Pacific whiting fillets.

	Fillet area examined					
	Nape		Middle		Tail	
	Dorsal	Ventral	Dorsal	Ventral	Dorsal	Ventral
Degree of white pseudocyst infection (%)/examination area						
None	38	41	41	43	46	46
Light (1-22)[1]	32	34	33	37	32	34
Moderate (23-87)[1]	18	15	17	13	15	13
Heavy (88 and over)[1]	12	11	9	8	8	8
Degree of black pseudocyst infection (%)/examination area						
None	41	34	43	40	44	41
Light (1-28)[1]	51	55	51	52	50	54
Moderate (29-79)[1]	6	8	4	6	5	3
Heavy (80 and over)[1]	2	3	2	2	1	2
Sensory texture(s) (%)/examination area						
Normal	77	82	81	85	85	87
Soft	12	10	11	10	10	10
Abnormal	11	8	8	5	5	4
Sample size	502	548	562	556	560	551

[1]Pseudocyst counts.

$P = 0.008$). Incidences of heavy infections of black pseudocysts were 2 to 3% at the nape and about 1 to 2% at the tail ($r = 0.71$ at $P = 0.06$). In general, there tend to be more black and/or white pseudocysts in the nape than in the tail area, although the correlation of white pseudocysts in the dorsal to ventral direction was rather low ($r = -0.21$ at $P = 0.035$).

Sensory texture profiles shown in Table 7 indicated that more abnormal textures were found in the nape area (11 to 8%) than in the tail area (5 to 4%) of the fish examined ($r = 0.48$ at $P = 0.16$).

Effect of Culling

At the present time, there is no accepted method or methods for efficiently detecting and culling Pacific whiting infected with white or black pseudocysts. Ultraviolet light and back lighting with white light have been tried on occasion, but these techniques have not been developed enough to be effective for use in Pacific whiting production. This leaves visual detection as the only on-site method for detecting and removing suspect Pacific whiting from the production line. However, as there are no reliable data available concerning the effectiveness of visual culling, an attempt was made in this study to estimate its potential usefulness.

Criteria for culling (Patashnik et al. 1982) in this study was described in a previous section. Of the 562 fish examined, 34 were visually culled on the basis of a moderate to heavy degree of white and black pseudocyst infection. Of these, 10 fillets were moderately to heavily infected with white pseudocysts, 7 with both black and white pseudocysts, and 17 with only black pseudocysts. Based on the criteria developed by Patashnik et al. (1982), these results suggest that culling fillets that are moderately or heavily infected with pseudocysts appears possible. However, since culling has not been successfully demonstrated in a commercial setting, the technique may prove to be too difficult and time consuming to be practical.

CONCLUSIONS

Overall, 18% of the Pacific whiting samples collected for this study were uninfected with *Kudoa*. Furthermore 65% had counts of <10 white pseudocysts, and only 10% had counts over 100 white pseudocysts. By comparison, 81% of the fish samples had <10 black pseudocysts counted and only 1% were infected with over 100 black pseudocysts counted.

When both the white and black pseudocyst counts were considered collectively, the variation in white pseudocysts explained 55% of the variation in sensory texture, whereas black pseudocysts accounted for 14%. However, when the effect of the white pseudocysts was mathematically removed from the fish samples having both, the black pseudocysts were found to explain only 1.5% of the variation in sensory texture.

Infections of white *K. paniformis* and white mixed infections correlated ($r = 0.80$ and 0.79, respectively) with the variations in sensory texture better than the black *K. paniformis* or black mixed infections (0.66 and 0.49, respectively). Neither the white nor the black *K. thyrsitis* pseudocyst counts correlated well with sensory textures. Although common in the Pacific whiting samples examined in this study, *K. thyrsitis* consistently were found in low numbers. On the other hand, *K. paniformis* were identified in 26% of the sample, and mixed infections were observed in 34% of the fish examined.

The heaviest infections of white and black *Kudoa* sp. pseudocysts were found in the Pacific whiting caught off the coast of California. The highest percentage of abnormal sensory textures were also observed in the fish harvested off the California coast.

Generally, in this study, we found that the larger the fish the greater the incidence of abnormal textures. Sex of the fish had no apparent effect on the quality of sensory texture.

Anatomically, the nape and dorsal areas of the Pacific whiting samples examined tended to have higher counts of white pseudocysts, and therefore more abnormal textures, than the other areas of the fish examined. The occurrence of heavy white pseudocyst infections in the nape, middle, and tail sections of the fish samples averaged 11.5%, 8.5%, and 8%, respectively. Heavy black pseudocyst infections were 2.5%, 2%, and 1.5% for nape, middle, and tail sections. Overall, abnormal textures were found 9.5% of the time in the nape, 6.5% in the middle, and 4.5% in the tail. Differences in the number of white pseudocyst counts found between the dorsal and ventral sides of the fish were small. The occurrence of abnormal texture was 30% greater for the dorsal side of the fish than the ventral side.

Results of visual culling in this study suggest that the method may have some potential, but

that the technique has yet to be successfully demonstrated under commercial conditions.

ACKNOWLEDGMENTS

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DISTRIBUTION AND ABUNDANCE OF BILLFISH LARVAE (PISCES: ISTIOPHORIDAE) IN THE GREAT BARRIER REEF LAGOON AND CORAL SEA NEAR LIZARD ISLAND, AUSTRALIA

JEFFREY M. LEIS,[1] BARRY GOLDMAN,[2] AND SHOJI UEYANAGI[3]

ABSTRACT

Istiophorid larvae were relatively common in plankton samples from the Lizard Island region in November to early March 1980-85. Black marlin, blue marlin, and sailfish larvae were captured. Larvae of all three taxa were most concentrated and abundant in the Coral Sea immediately seaward (= windward) of the outer ribbon reefs. Concentration and abundance within the Great Barrier Reef Lagoon were not usually different from those more than 0.25 nautical miles offshore in the Coral Sea. Size-frequency data combined with the distributional information suggest that spawning or at least hatching of eggs was concentrated in the area within 0.25 nautical mile seaward of the reef crest. Preflexion larvae of blue marlin and sailfish were essentially confined to the upper 6 m of the water column (and perhaps the upper half of that), but not the neuston. Preflexion larvae of all three species dominated the oblique bongo net tows (98%), while postflexion larvae dominated the neuston samples (76%). This suggests an upward ontogenetic movement.

The horizontal distribution of istiophorid larvae is probably the result of spawning close to the reef front, an area of supposed downwelling, combined with the proclivity of the larvae to occupy surface waters. This should lead to retention of larvae in the forereef area. Some caveats about accepting this hypothesis as a complete explanation for the horizontal distribution of istiophorid larvae are discussed.

Near-reef areas appear to be important in the early life history of istiophorids at least in the Coral Sea and for the three taxa studied.

The billfishes of the family Istiophoridae are large, high trophic level, pelagic fishes of considerable sport and commercial importance throughout tropical and subtropical oceans (Nakamura 1985). Information on their early life history is limited and investigations have been hampered by the relative rarity of the larvae. Studies on the distribution of istiophorid larvae in the Indo-Pacific have dealt with distributions over very broad areas and have not examined distributions on a small scale, particularly those very close to reefs. (The considerable Japanese work was summarized by Nishikawa et al. 1985 and the Russian work by Gorbunova 1976.) Size of larvae in relation to horizontal distribution has only rarely been considered. Aside from reports that istiophorid larvae had been captured in neuston tows (e.g., Bartlett and Haedrich 1968; Gorbunova 1976) the only published information on vertical distribution of istiophorid larvae was provided by Ueyanagi (1964), who concluded billfish larvae were largely confined to surface waters during the day and dispersed through the upper 50 m at night.

During studies on the distributional ecology of the larvae of reef fishes in the vicinity of Lizard Island in the northern region of the Great Barrier Reef, Australia, two of us (Leis and Goldman) have sampled extensively in the Great Barrier Reef Lagoon and the near-reef waters of the Coral Sea. In our samples, we captured a relatively large number of istiophorid larvae. This has provided information which sheds light on little known aspects of the early life history of istiophorids and in view of the widespread interest in istiophorid biology, we have prepared this summary on the horizontal and vertical distribution of istiophorid larvae over relatively small scales and how these relate to development of the larvae. Because istiophorid larvae are difficult to identify, we have collaborated to insure accuracy in identification of the larvae.

[1]Division of Vertebrate Zoology, The Australian Museum, P.O. Box A285, Sydney South, NSW 2000, Australia.
[2]Lizard Island Research Station, PMB 37, Cairns, Queensland 4870, Australia; present address: Research Associate, The Australian Museum, P.O. Box A285, Sydney South, NSW 2000, Australia.
[3]Faculty of Marine Science and Technology, Tokai University, 3-20-1 Orido, Shimizu, Shizuoka 424, Japan.

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MATERIALS AND METHODS

All samples considered here were taken in an area between Lizard Island, approximately midway across the Great Barrier Reef Lagoon, to 10 nmi seaward of the outer ribbon reefs of the Great Barrier Reef in the Coral Sea (Fig. 1).

The Great Barrier Reef Lagoon is modally 30 m deep in this region (range 25-40 m). The outer ribbon reefs are located along the shelf break, and the bottom falls off sharply with distance into the Coral Sea reaching depths >2,000 m within 6 nmi (Fig. 1).

The samples immediately to windward of Lizard Island were taken from a 7 m boat with a net of 0.4 m^2 mouth area (see Leis 1986 for further details of sampling). Other samples were taken from RV *Sunbird*, a 14 m catamaran. The neuston net, with mouth dimensions of 1 × 0.3 m and 0.5 mm mesh, was towed between the bows of the catamaran, and normally fished to a depth of 0.1 m. Bongo nets of 0.85 m diameter and fitted with a depressor were towed in a double-oblique pattern to study horizontal distribution or in opening-closing mode to study vertical distribution. Nets were towed at approximately 1 m/second, were of 0.5 mm mesh, and were equipped with a flowmeter. During the vertical distribution study, a depth sensor with a deck display was fitted to the net. At other times, a mechanical depth-distance recorder was used.

The neuston net, when used, fished during the bongo net tow. The oblique bongo net tows were done to the greatest calculated depth that was

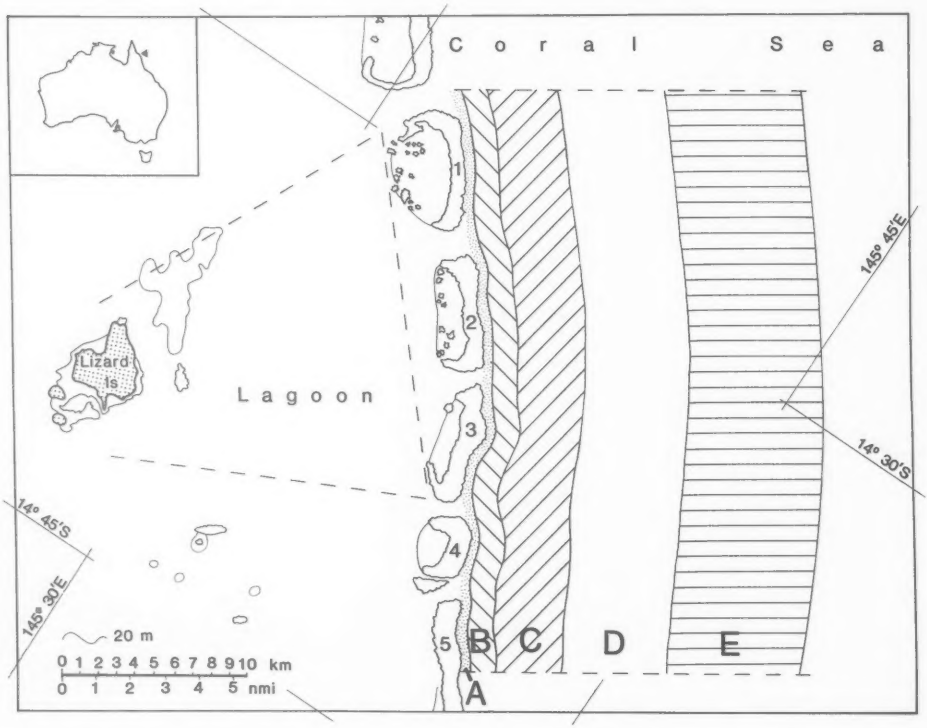

FIGURE 1.—Map of the study area. One sampling block is the Great Barrier Reef Lagoon beween Lizard Island and the ribbon reefs, this is delineated by the broken lines. In the Coral Sea, there are five sampling blocks A-E as defined in the text. Depths in the Lagoon range from 20 to 40 m. Depths to 400 m are encountered in Coral Sea block A, to 1,000 m in block B and >1,500 m in C-E. Outer ribbon reefs are 1) Day, 2) Carter, 3) Yonge, 4) No Name, and 5) Number 10 Ribbon. None of the outer reefs are emergent.

considered safe in the lagoon and close to the windward face of the reef. Because of the great variations in bottom topography in the latter area, the net actually hit bottom upon occasion. Further offshore, bongo net tows were done with a standard amount of wire out which ensured a maximum sampling depth in excess of 100 m.

Position fixing in the Coral Sea was by radar reflection of the waves breaking on the reef crest when close to the reef. This meant that actual distance off the reef varied somewhat (~100 m) depending on sea state and tide. Four cruises were made to investigate horizontal distribution: 1) 2-5 November 1984, 2) 17 and 20-22 November 1984, 3) 30 January-2 February 1985, and 4) 9-13 February 1985. On each cruise, six samples were taken between Lizard Island and the outer reef on one day (Fig. 1), and three days were spent in the Coral Sea running a transect each day and starting at opposite ends of the transect on alternate days. On each transect, two randomly located samples were taken in each of five offshore blocks defined by distance (nmi) from the outer reef crest (Fig. 1): A, 0-0.25 nmi; B, 0.25-1.0 nmi; C, 1.0-3.0 nmi; D, 3.0-6.0 nmi; E, 6.0-10.0 nmi. Therefore, six samples were taken in each block on each cruise. The three transects on a cruise were each centered off a different reef (i.e., either of Day, Carter, Yonge, No Name, or Number 10 Ribbon Reefs). Bad weather and high volumes of floating pumice precluded the routine use of the neuston net. There were some variations in this plan owing to weather or equipment problems, the most serious of which was missing 4 of 6 samples in block A on the second cruise. Larvae from other samples taken with similar methods in November 1983 were also included where appropriate. Funding limitations prevented processing of samples from block D.

The vertical distribution samples were taken in the lee of Carter Reef primarily in the Great Barrier Reef Lagoon, but partially in the pass to the north of Carter Reef (Fig. 1). Samples were taken in sets; each set consisted of a neuston tow and 3 bongo net (0-6 m, 6-13 m, and 13-20 m) tows. The 0-6 m stratum was sampled in the undisturbed water flowing between the hulls of the catamaran. In February-March 1983, 22 such sets were taken, 8 each in morning and afternoon and 6 at night.

Additional samples from within the Great Barrier Reef Lagoon as reported by Leis and Goldman (1984, 1987) and Leis (1986) were used for seasonality information. Samples in the Lagoon were taken in all months but May, June, August, September, and December. Samples were taken in the Coral Sea in October, November, January, and February.

Oblique bongo net tows typically filtered 1,000-1,500 m^3 and horizontally stratified tows filtered 400 m^3. Neuston tows typically travelled 1,200-2,000 m. All nets were carefully washed after each tow and the sample preserved in 5-10% seawater-formalin.

In the laboratory, samples were sorted using a dissection microscope (~10×) and all larvae removed. Samples from both sides of the bongo net were fully sorted except for the Great Barrier Reef Lagoon samples from February-March 1983 and November 1984 when only side was sorted because of high plankton volume. Larvae were placed in 70% ethanol prior to measurement. Identification of larvae followed Ueyangi (1963, 1974a, b). Larvae were measured using an eyepiece micrometer of a dissection microscope to the nearest 0.1 mm. Notochord length and standard length were measured for preflexion and postflexion larvae, respectively (Leis and Rennis 1983). Larvae from these samples are deposited in the Australian Museum, Sydney.

Numbers of larvae per sample were converted to numbers per volume (concentration) and numbers per area (abundance) using standard methods (Leis 1986). In analysis of vertical distribution data, only positive sets (i.e., those in which at least one larva was captured) were considered. Statistical methods followed Conover (1971) and Zar (1974). References to the Student-Newman-Keuls (SNK) test refer to the version based on ranks (Zar 1974).

RESULTS

Identification

We captured larvae of black marlin, *Makaira indica*; blue marlin, *Makaira mazara*; striped marlin, *Tetrapturus audax*; and Indo-Pacific sailfish, *Istiophorus platypterus*. The larvae here identified as black marlin correspond to the "non-pigmented" sailfish of Ueyanagi (1974a, b). This type of istiophorid larva has been captured only in the seas off northern Australia and the southern portion of the Indonesia-New Guinea archipelago (Ueyanagi 1974a, b). In our Coral Sea samples these larvae were found almost exclusively during November, the time when large

numbers of gravid female black marlin occur in the area (B. Goldman pers. obs.; J. Pepperell[4]). A major sport fishery is based on this apparent spawning migration and the catches are made primarily just off the windward reef faces in the northern Coral Sea. When sampling in November 1984, our research vessel was frequently operating in the midst of the sport fishing fleet. This circumstantial evidence suggested the possibility that the "non-pigmented" sailfish larva was in fact the larva of the black marlin, and led us to recheck these "non-pigmented" sailfish larvae. Two specimens (5.6 and 9.7 mm) were cleared and stained for bone and cartilage (Potthoff 1984); both specimens had vertebral formulae of 11+13=24. This confirms that they are of the genus *Makaira* (Nakamura 1985). These larvae can be distinguished from those of the only other Indo-Pacific member of the genus, the blue marlin, by head profile and depth and minor pigment differences. Therefore, we concluded that the "non-pigmented" sailfish larva captured in the present study were black marlin. A more detailed treatment of the identity of "non-pigmented" sailfish larvae will be given separately (Ueyanagi and Leis in prep.).

The larvae identified here as sailfish are normally pigmented sailfish larvae which had not previously been reported from the Coral Sea (Ueyanagi 1974a, b). Only a few striped marlin larvae were captured, and because nearly all were small and only tentatively identified, they are not considered further.

Seasonal Occurrence

Sailfish larvae were taken only in January, February, and March. Blue marlin larvae were taken in mid-November, January, February, March, and April, although only one larva was taken in April. Black marlin larvae were taken throughout November, and three were taken in January-February.

A sequence of occurrence of larvae and presumably of spawning in the area begins with the appearance of black marlin larvae in late spring-early summer, followed by blue marlin in summer-autumn, and finally sailfish in late summer-early autumn.

Horizontal Distribution

Black marlin larvae were most concentrated in block A adjacent to the seaward side of the reef on all cruises (Table 1). Concentrations elsewhere were low, with median values usually of zero. However, data from only one cruise could be tested statistically. The distribution of abundance was similar to that of concentration, with the exception that abundance in the two near-reef blocks could not be shown to be significantly different during the first cruise. During the first two (November) cruises, black marlin larvae were taken in 7 of 8 samples from the near-reef area (block A). Only three black marlin larvae were taken on cruises three and four (January-February), all in block A. Black marlin larvae were present in only 13 of 96 samples taken elsewhere, and of these areas, block B (0.25-1.0 nmi offshore) had the highest frequency of occurrence, 5 of 24 samples.

Clearly, black marlin larvae were consistently found in greatest numbers closest to the seaward side of the reef. The offshore extent of this high density zone of black marlin larvae was very limited, extending at most to 1 nmi seaward (block B) of the reef crest, but more likely to only 0.25 nmi.

Blue marlin larvae were less abundant than black marlin in our samples but had a similar distributional pattern. Again, data from only one cruise (the third) could be tested statistically. Except for the second cruise, blue marlin larvae were both most concentrated and abundant in block A, the area closest to the seaward face of the reef (Table 1). Further, 8 of the 13 occurrences were in this block. During the second cruise, blue marlin larvae seemed most concentrated and abundant at block B (0.25-1.0 nmi off), but only six larvae were captured on this cruise and only two samples were taken in block A so the significance of these results is questionable. Blue marlin were, with the possible exception of the second cruise, consistently found in greatest numbers closest to the seaward side of the reef. This is similar to the pattern for black marlin. However, small numbers of blue marlin larvae were captured in block E, the most offshore segment of the transect, and this offshore area had the second highest frequency of occurrence of blue marlin larvae (Table 1).

Only 13 sailfish larvae were taken, and the data are too sparse to indicate much more than all but 1 of the 7 occurrences were in the two blocks nearest the reef front (A and B). Sailfish larvae

[4]J. Pepperell, Fisheries Research Institute, N.S.W. Department of Agriculture, Cronulla, N.S.W., Australia, pers. commun. 1986.

TABLE 1.—Distribution of istiophorid larvae based on transects from the Great Barrier Reef Lagoon into the Coral Sea. Co, concentration (larvae/1,000 m³); Ab, abundance (larvae/100 m²); f, frequency (i.e., number of positive hauls). Values for Co and Ab are medians, and parenthetically, ranges. P is for Kruskal-Wallis test. For tested data sets, values with the same superscript symbol (# or †) are not significantly different ($P > 0.05$, SNK Test). NT, not tested statistically: T, because only 2 samples were taken in block A; F, because too few larvae were taken. Normally, 6 samples were taken in each block on each cruise. No larvae were taken on the cruises not listed.

		Coral Sea blocks				
	Great Barrier Reef Lagoon	A (0-0.25 nmi)	B (0.25-1.0 nmi)	C (1.0-3.0 nmi)	E (6.0-10.0 nmi)	P
Black marlin						
1st cruise						
Co	0 (0-4.4)#	3.8 (0-11.3)	0.8 (0-1.9)#	0 (0-1.9)#	0 (0-0.5)#	0.04
Ab	0 (0-10.9)#	15.0 (0-56.5)†	10.5 (0-33.0)#†	0 (0-47.1)#	0 (0-13.0)#	0.06
f	1	5	4	2	2	
2d cruise						
Co	0 (0-1.4)	2.8 (1.1-4.5)	0 (0-0.5)	0 (0-1.2)	0	NT, T
Ab	0 (0-3.4)	12.8 (5.1-20.4)	0 (0-6.9)	0 (0-14.9)	0	
f	2	2 (of 2)	1	1	0	
3d cruise						
Co	0	0 (0-0.7)	0	0	0	NT, F
Ab	0	0 (0-2.0)	0	0	0	
f	0	2	0	0	0	
4th cruise						
Co	0	0 (0-1.2)	0	0	0	NT, F
Ab	0	0 (0-1.8)	0	0	0	
f	0	1	0	0	0	
Blue marlin						
2d cruise						
Co	0	0	0 (0-2.2)	0 (0-0.6)	0	NT, T, F
Ab	0	0	0 (0-23.0)	0 (0-7.2)	0	
f	0	0 (of 2)	2	1	0	
3d cruise						
Co	0#	1.5 (0-8.4)	0 (0-0.5)#	0#	0 (0-0.6)#	0.02
Ab	0#	12.6 (0-25.2)	0 (0-5.2)#	0#	0 (0-7.0)#	0.02
f	0	5	1	0	2	
4th cruise						
Co	0	0.33 (0-2.4)	0	0	0 (0-1.8)	NT, F
Ab	0	1.0 (0-7.7)	0	0	0 (0-21.1)	
f	0	3	0	0	2	
Sailfish						
3d cruise						
Co	0	0 (0-4.2)	0 (0-0.6)	0	0	NT, F
Ab	0	0 (0-12.6)	0 (0-6.1)	0	0	
f	0	1	2	0	0	
4th cruise						
Co	0	0 (0-2.6)	0 (0-0.8)	0 (0-0.7)	0	NT, F
Ab	0	0 (0-10.4)	0 (0-9.3)	0 (0-7.8)	0	
f	0	2	1	1	0	

may have a distribution similar to that of blue marlin and black marlin larvae (Table 1).

Sizes of Larvae From Bongo Net Tows

Black marlin larvae ranged from 2.5 to 6.8 mm with a strong mode at 2.8-2.9 mm (Table 2a). Statistical comparison of the size-frequency data between areas could only be undertaken for the first cruise. Data from block A were compared with data from all other areas pooled. The size-frequency distributions were possibly different (Kolmogorov-Smirnov test, $P = 0.07$): a greater proportion of the larvae were of the smaller size classes (<4 mm) in block A than in the other blocks. Inspection of the limited size-frequency data from the other cruises indicates a similar situation. More than one cohort of larvae was present because larvae on the second cruise were not larger than those on the first.

Blue marlin larvae ranged from 2.5 to 8.3 mm with a weak mode at 3.1 mm (Table 2b). Too few blue marlin larvae were captured to allow rigorous analysis of the size-frequency data, but there did not appear to be any difference in the size

TABLE 2.—Size frequency of a) black and b) blue marlin and c) sailfish larvae. If a block or cruise is not listed, no larvae were taken there. X indicates a hiatus in the size sequence. A few larvae too badly damaged to be measured were omitted. Blanks indicate zero.

a. Black marlin

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0	4.5	5.0	X	5.6	5.7	5.8	5.9	6.0	X	6.8
E	1st		1 1												
C	1st		1 1 1			1									
	2d		1 1												
B	1st		1 1 1 1			1	1					1			1
	2d	1	1												
A	1st	3 2 8 6	4 3 2 1 3	4	3 1	1	1		1		1				
	2d	1 3 1 2 3													
	3d	1													
	4th	1	1												
Lagoon	1st			1	1		1								
	2d	1		1											

b. Blue marlin

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0	4.5	5.0	5.5	X	8.3
E	3d	2								
	4th	1			1 1 1					1
C	2d		1							
B	2d	1 1 1				1				
	3d				1					
A	3d	2 1 1	4 2 1 2		1 1	1 1	1 1			
	4th		1			1	1	2		

c. Sailfish

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0
C	4th			1	
B	3d		1 1		
	4th		1		
A	3d	2 3	1		
	4th		1 1 1		

composition of the larvae between areas. Larvae on the fourth cruise were apparently larger than those on the third, however it is doubtful that only one cohort was involved because of the small size difference between the two cruises which were about 10 days apart (Table 2b).

Sailfish larvae ranged from 2.5 to 3.8 mm, with a mode at 2.6 mm (Table 2c). Only 12 larvae were captured, but there is a suggestion that smaller larvae were taken nearest the windward reef face, and that the size of larvae increased with distance into the Coral Sea.

Vertical Distribution

Our information on vertical distribution comes primarily from samples taken within the Great Barrier Reef Lagoon. It is limited, but it is consistent.

In the sampling with opening-closing bongo net and neuston net, larvae of two species, sailfish and blue marlin, were captured. No istiophorid larvae were present in the neuston tows of the vertical distribution sets. Sailfish larvae were captured in 7 of 16 day-time vertical sets and none of the 6 night-time sets. All the sailfish larvae were captured in the 0-6 m stratum with the exception of two larvae, one from each of the two deeper strata, which came from two sets taken in one of the turbulent interreef channels during a falling tide (Table 3). Even with the inclusion of the data from the interreef channel, sailfish larvae were most concentrated in the 0-6 m stratum while concentrations in the other strata did not differ (Friedman test, SNK test, $P < 0.05$). Blue marlin larvae were captured in only three of the day-time vertical sets. All the blue marlin larvae were captured in the 0-6 m stratum, with the

TABLE 3.—Day-time vertical distribution of sailfish and blue marlin larvae in the vicinity of Carter Reef in February and March 1983. *N* refers to number of vertical sets (i.e., a tow in each stratum) that contained at least one larva of that species.

Sailfish ($N = 7$)

Depth stratum	Concentration (larvae/400 m³) Median	Range	Number of positive hauls (of 7)
Neuston	0	0-0	0
Bongo net			
0-6 m	1.7	0-7.8	6
6-13 m	0	0-1.6	1
13-20 m	0	0-1.0	1

Blue marlin ($N = 3$)

Depth stratum	Concentration (larvae/400 m³) Median	Range	Number of positive hauls (of 3)
Neuston	0	0-0	0
Bongo net			
0-6 m	1.8	1.8-4.3	3
6-13 m	0	0-0	0
13-20 m	0	0-1.0	1

exception of a single larva from 13 to 20 m from one of the interreef channel sets. In the three positive sets, blue marlin larvae were always most concentrated in the 0-6 m stratum, but there were too few data for rigorous testing.

Blue marlin and sailfish larvae occurred in one vertical set taken on the windward side of Lizard Island in January 1980 (see Leis 1986). One larva of each species was taken in each of the 0-1 m and the 3-4 m tows, while none were taken in the 6-7 m tow.

Istiophorid larvae from our neuston samples were developmentally more advanced (older) than those from bongo net samples. In all our samples, the bongo net captured 160 istiophorid larvae (black marlin, blue marlin, sailfish), three of which were postflexion stage, while the neuston net captured 17 istiophorid larvae (black marlin and blue marlin), 13 of which were postflexion stage (chi square, $P < 0.001$).

During the day preflexion blue marlin and sailfish larvae inhabit the upper 6 m, and possibly the upper half of that, but not the neuston. It appears that once the caudal fin is formed, istiophorid larvae move upward even more and enter the neuston.

DISCUSSION

Distribution of istiophorid larvae over such a small scale has not been studied previously, nor have such high concentrations of larvae been reported. Our results were surprising. Highest concentrations and abundances of istiophorid larvae in our study area were consistently found in the Coral Sea very close to the windward side of the ribbon reefs at the outer edge of the Great Barrier Reef. The size-frequency data (see below) suggest that this near-reef environment was a spawning area or just down wind of one for the three types of billfishes considered here.

Concentration and abundance of istiophorid larvae in the Great Barrier Reef Lagoon (hereafter referred to as the Lagoon) were always lower than in block A when both areas were sampled, but lagoonal numbers were generally not different from those further offshore in the Coral Sea. We cannot exclude the possibility that some istiophorid spawning takes place within the Lagoon, but believe it is more likely that the larvae were advected into the Lagoon through the interreef channels, as are larvae of many other oceanic fishes (Leis 1986; Leis and Goldman 1987). Still, concentrations of istiophorid larvae were high at times in the Lagoon (e.g., February-March 1983), and the relative survival of the larvae in the Lagoon vs. the Coral Sea is an open question.

The marginally significant difference between areas in size frequency of black marlin larvae suggests that hatching of the eggs takes place very near the windward face of the reefs. This also suggests that black marlin larvae found elsewhere were largely the result of dispersal away from the near-reef area, and these dispersed larvae had grown somewhat during their dispersal. Spawning could either be concentrated in the near-reef area or more widely spread, in which case the eggs would have become concentrated in the near-reef area through wind-induced surface drift and forereef downwelling (see below). Alternatively, larval growth rates could be higher or mortality lower in the areas further from the reef. Our data do not allow us to distinguish between these alternatives, but we believe the first is the most likely.

The data on blue marlin larvae gave no indication of differences in size frequency between areas. The lack of difference in size-frequency distribution could indicate that spawning in blue marlin was more evenly spread than in black marlin. If so, the increase in numbers nearest the windward side of the reef would be attributable to concentration and retention of larvae there. We cannot differentiate between this possibility and

the alternative that spawning is most intense near the reef.

Too few sailfish larvae were taken to make any firm statements on distribution of larvae of different sizes. However, they appeared to have a pattern of size distribution with location similar to that of black marlin larvae.

The vertical distribution data show that, at least during the day, preflexion larvae of blue marlin and sailfish concentrate in the upper few meters (perhaps upper 3 m) of the water column, but not in the neuston. However, postflexion larvae of blue marlin and black marlin are neustonic. This ontogenetic vertical migration has not been noted previously. The somewhat different results from the limited interreef channel samples could have been caused by turbulence due to strong tidal currents in these narrow passes.

Using nonclosing nets, Ueyanagi (1964) studied vertical distribution of istiophorid larvae (all taxa combined) over the upper 50 m and concluded that during the day larvae were most often caught at the surface and frequency of capture decreased with depth. At night catches of larvae were approximately evenly distributed over the upper 50 m. More recent data (Ueyanagi unpubl. data) confirmed this pattern for blue marlin, striped marlin, spearfish, and sailfish larvae.

It is possible that the observed horizontal distribution of istiophorid larvae in the Lizard Island area results solely from a concentration of spawning or at least hatching of eggs close to the windward side of the reefs. However, it is likely that additional factors are involved. The southeast trade winds push surface water against the windward sides of these reefs and although some of the water flows across the reefs into the Lagoon, downwelling (anstau conditions) should occur seaward of the reef. An organism which maintains a position near the top of the water column, as do the istiophorid larvae (or positively bouyant fish eggs), would accumulate in such a downwelling zone. A similar situation has been described off the windward reef at Lizard Island where larvae of a number of reef fishes with shallow-living larvae were apparently retained (Leis 1986). However, the istiophorid larvae apparently disperse away from the surface at night (Ueyanagi 1964) whereas the larvae retained off windward Lizard Island tended to maintain their day-time vertical distribution at night (Leis 1986). If they did leave the surface, the istiophorids might be advected away from the reef front. A further caveat against accepting the "anstau hypothesis" as a full and simple explanation for the distribution of istiophorid larvae in the area involves the trade winds. During the time the near-reef peak in istiophorid larvae was best developed (2-5 November), the winds varied from 0 to 10 kt and from northeast to southeast while on the other cruises, the wind was stronger and varied from 10 to 30 kt and from east to southeast. Finally, preliminary analysis of data from the samples in which the istiophorids were captured revealed that high abundances of a number of reef fish larvae also occur off the windward reef face. Many of these were not near-surface dwelling larvae. Further study of larval fish distributions and their causes in this area is clearly required.

Whatever the causes for the distributions of the istiophorid larvae very near the windward reef face, it is somewhat surprising that the larvae of epipelagic, oceanic fishes should be so abundant in such a narrow band along the reefs. Sailfish are known to spawn relatively close to land masses rather than in the open ocean (Ueyanagi 1974c) and black marlin are often found nearshore (Nakamura 1985); blue marlin are truly oceanic fishes (Nakamura 1985; Nishikawa et al. 1985). Yet larvae of all three were concentrated in a narrow band only 0.25 nmi (possibly to 1 nmi) off the reef crest. If pelagic fishes such as istiophorids concentrate their spawning very close to reefs or if the larvae are retained there, it will be essential for such areas to be included in studies of the larval biology of these fishes. The assumption that open oceanic areas are the important nursery areas for epipelagic fishes seems at best questionable for istiophorids in the Coral Sea and similar factors may apply to other taxa in this and other areas. For example, Miller (1979) reported much higher concentrations of yellowfin tuna larvae, *Thunnus albacares*, in areas 200 m off the Oahu shoreline than had been reported elsewhere.

Nearshore or near-reef areas may provide more favourable habitats for fish larvae, including those of many pelagic species, than do oceanic areas. The larvae of jack mackerel, *Trachurus symmetricus*, an epipelagic (albeit, neritic) fish, are spread widely over oceanic and coastal areas off California, yet larval mortality due to starvation in oceanic areas can be much higher than in coastal areas, presumably because of insufficient concentrations of food offshore (Theilacker 1986). This may apply to other pelagic fishes as well and

is a further indication that very nearshore (and near-reef) areas must not be excluded from studies of the larvae of epipelagic fishes.

In summary, we found the highest concentrations and abundances of istiophorid larvae of three taxa very close to the windward face of the Great Barrier Reef in the Coral Sea in late spring and summer. Size-frequency analysis suggested that these high concentrations of larvae were due to spawning or at least hatching of eggs very close to the reef. The larvae might be retained in this forereef area of supposed downwelling because, at least during the day, they concentrate in the upper few meters of the water column as preflexion larvae and in the neuston as postflexion larvae. These results have potentially important implications for the study of the larval biology of epipelagic fishes.

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PREVALENCE AND EFFECTS OF INFECTION OF THE DORSAL AORTA IN YELLOWFIN TUNA, *THUNNUS ALBACARES*, BY THE LARVAL CESTODE, *DASYRHYNCHUS TALISMANI*

RICHARD W. BRILL,[1] ROBERT BOURKE,[1] JAMES A. BROCK,[2] AND MURRAY D. DAILEY[3]

ABSTRACT

Approximately 60% of small (<3 kg) yellowfin tuna, *Thunnus albacares*, caught near the Hawaiian Islands carry the plerocercoid (larval) stage of the cestode (tapeworm), *Dasyrhynchus talismani*, in their anterior dorsal aortas. Because the worms and the resultant host inflammation appear to occlude the vessel almost totally, we assumed that the parasite could increase natural mortality rates. Tuna could be limited in their ability to capture prey and therefore should show evidence of long- or short-term food deprivation. We measured body weight, fork length, liver weight, heart weight and, in fish captured from one school, RNA/DNA ratios (a measure of short-term growth rate), and otolith weight (a measure of long-term growth rate) from parasitized and unparasitized fish. We found no significant differences between infected and uninfected fish nor any evidence of starvation in infected fish. How small yellowfin tuna remain apparently unaffected by the parasitic occlusion of their dorsal aorta remains to be demonstrated.

We also examined changes in incidence of infection in small yellowfin tuna caught between February 1985 and March 1986 as well as the prevalence in large (>45 kg) fish. Large yellowfin tuna were rarely parasitized (5.2%) in the dorsal aorta, but showed a high rate (>80%) of infection within other major arteries. The prevalence in small fish varied dramatically with season, dropping suddenly from 66% in June-July 1985 to 11% in August-September 1985. Unparasitized fish caught during August-September 1985 showed significantly higher condition factors, relative heart weights, and relative liver weights than did unparasitized fish caught at other times of the year. We hypothesize that the sudden decrease in prevalence was due to influx of a separate group of small yellowfin tuna into the Hawaiian fishery. We believe that this parasite may therefore serve as a marker for tracing the movements of small yellowfin tuna into and out of specific fisheries or areas.

During a series of experiments that involved catheterization of the anterior dorsal aorta of small (1-3 kg) yellowfin tuna, *Thunnus albacares*, we discovered that approximately 60% of the experimental fish had this blood vessel infected with parasites. The parasites were white, round (2-4 mm in diameter), often more than 4 cm long, and usually folded repeatedly. As a result of the parasites and the tissue inflammation that develops as part of host immune response, the lumen of the infected aortas appeared almost totally occluded. Because all the blood to the internal organs and swimming muscles must flow past this occlusion, we assumed the parasite could be a major factor contributing to the natural mortality of small yellowfin tuna.

The first demonstration of a dorsal aorta parasite in yellowfin tuna was by Kishinouye (1923), who stated, "Often a species of nematod [sic] is found in the dorsal aorta of *Neothunnus macropterus* [now *Thunnus albacares*]; the parasite causes the tissues of the canal to become thick and tough, giving it at the same time a yellowish tint." Other investigators described intravascular parasites from the branchial vessels and arteries serving the stomach, liver, spleen, pyloric caecum, and gall bladder of this species (Baudin Laurencin 1971). The parasites have been described simply as the plerocercoids (larval cestodes) (Chen and Yang 1973), identified to the family Dasyrhynchidae (Ward 1962), or as the species *Dasyrhynchus talismani* (Baudin Laurencin 1971).

Intravascular infection by plerocercoids has been reported from yellowfin tuna caught in the western Pacific (Chen and Yang 1973), eastern Atlantic (Baudin Laurencin 1971), Gulf of Mexico (Ward 1962), and now central Pacific (this report). Infection rates have been reported to be as high as 100% (Baudin Laurencin 1971). If all re-

[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.
[2] Aquaculture Development Program, Department of Land and Natural Resources, State of Hawaii, Honolulu, HI 96819.
[3] Southern California Ocean Studies Consortium, California State University, Long Beach, Long Beach, CA 90840.

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ports involve the single parasite species, *D. talismani*, this parasite is both common and ubiquitous.

Because of the apparent vessel blockage by parasites and tissue inflammation, we hypothesized that infected fish would be severely activity limited and not function well as predators. If so, infected fish should show evidence of short- and/or long-term food deprivation, including lower relative condition factors, smaller livers, and slower long- and short-term growth rates (Bulow 1970; Pollard 1971, 1973; Bulow et al. 1981). We also expected blockage of the dorsal aorta to cause increased blood pressures, increased cardiac work, and therefore cardiac hypertrophy (Poupa and Ostadal 1969).

To test our hypotheses, we measured fork length, body weight, liver weight, and ventricle weight from parasitized and unparasitized fish. We also determined RNA/DNA ratios as a measure of the parasite's effects on short-term growth rates (Bulow 1970; Bulow et al. 1981), and relative otolith weights as a measure of the parasite's effects on long-term growth rates. Since otolith weights are linearly related to a fish's chronological age (Boehlert 1985), fish that are older at a given body size should have relatively heavier otoliths. We also recorded the prevalence of infection in small (<3 kg) and large (>45 kg) yellowfin tuna, and in skipjack tuna, *Katsuwonus pelamis*, kawakawa, *Euthynnus affinis*, and bigeye tuna, *T. obesus*. Additionally, monthly prevalence in small yellowfin tuna was noted.

To measure directly the effect of the occlusion caused by the parasites and host inflammation, we used an in vitro perfusion test. We measured the pressure required to push various saline flow rates down the dorsal aorta in freshly dead infected and uninfected fish.

MATERIALS AND METHODS

Sampling Procedures

The small tunas (0.2-3 kg body weight) used in this study were captured at sea near Oahu, HI, returned alive to be held in shoreside tanks at the Kewalo Research Facility (National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory), or sacrificed at sea and held on ice. During necropsy, fork length and body weight were measured, ventricles and livers were removed, blotted dry, and weighed to the nearest 10 mg. Only those fish in captivity for 3 days or less were included in the data for condition factor, and relative heart and liver weights. Large yellowfin tuna (>45 kg body weight) were examined at the Honolulu Fish Auction for the presence of dorsal aorta parasites while the fish were being prepared for sale. All fish were examined within 24 hours of death.

Thirty-five live yellowfin tuna, from one school, were caught 15 January 1986 and transported alive to the Kewalo Research Facility. Immediately upon arrival, the animals were sacrificed, weighed, and measured. Lateral white muscle samples were taken within 4 minutes of death and immediately frozen on dry ice. These samples were subsequently used for measurement of RNA/DNA ratios using the Schmidt-Thannhauser procedure as described in Murno and Fleck (1966). The ventricles and livers of the fish were also removed, blotted dry, and weighed to the nearest 10 mg. Sagittal otoliths were removed, cleaned, dried, and weighed to the nearest microgram.

Parasites for species identification were obtained most often from the major artery within the spleen of large (>45 kg) yellowfin tuna. After being removed from a surrounding capsule, parasites were placed in tap water until the holdfasts everted.

For histological examination, sections of dorsal aorta were fixed in 10% buffered formalin and processed by routine laboratory procedures. Tissue sections were stained with hematoxylin and eosin.

Direct Measurement of Pressure-Flow Relationships in the Anterior Dorsal Aorta

To quantify blockage, we choose to measure the pressures required to push various flow rates of saline through the anterior dorsal aorta of infected and uninfected fish. The dorsal aorta of freshly killed fish was exposed from the confluence of the efferent arteries of the first and second gill arches to the point where it enters the first hemal arch. All efferent and afferent vessels were tied off except for the confluence of the efferent arteries from either the left or right first and second gill arches. This portion of the vessel was cut and a short length of flared polyethylene tubing (PE160, 2.4 mm OD) inserted. The dorsal aorta was also transected at the point where it entered the first hemal arch to allow the saline perfusate to flow out. Parasites were never found poste-

rior to this point. Saline perfusion pressures, at various constant flow rates provided by an infusion pump, were recorded via a Uonix[4] pressure transducer.

Calculation of Relative Condition Factor and Relative Organ Weights

Use of relative condition factor, and relative organ and otolith weights allow groups of fish containing individuals of a range of body sizes to be directly compared (Pollard 1972). Using data from unparasitized fish, regressions of body weight (g) on fork length (cm), liver weight (g) on body weight (g), and heart weight (g) on body weight, were fitted by a least squares technique to the exponential equation:

$$Y = a \cdot X^b$$

using a log-log transformation of the data. Relative condition factor and relative organ weights for individual fish were calculated using the regression parameters (a, b) with the equation:

$$K = W/a \cdot X^b.$$

For relative condition factor, W = body weight and X = fork length. For relative organ weights, W = liver or heart weight, and X = body weight.

The relationship of otolith weight (mg) to body weight was found best fit with the simple linear regression:

$$Y = a + (b \cdot X).$$

Relative otolith weights were therefore calculated using the equation:

$$K = W/(a + b \cdot X)$$

where W = otolith weight and X = body weight.

A relative condition factor <1 indicates that an individual is lighter for its fork length than predicted based on data from unparasitized fish. Similarly, a relative liver or heart weight <1 indicates a smaller liver or heart for a given body size than that found for unparasitized fish. A relative otolith weight >1 means that an individual experienced a relatively slower long-term growth rate (i.e., is relatively older for a given body size and therefore has a larger otolith).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Identification of the Parasite

Tapeworms (class: Cestoda, order: Trypanorhyncha) can be identified to species based on scolex morphology and tentacular hooks (onchotaxy), mature segments are not required. The larval cestodes recovered from the yellowfin tuna during this study showed proboscis chainettes flanked by a single row of intercalary hooks, a characteristic that distinguishes *Dasyrhynchus talismani* from its congeners.

This parasite was originally described from five mature worms removed from the spiral valve of *Galeus glaucus* (= *Prionace glauca*, the blue shark) off Cape Verde, West Africa (Dollfus 1935). *Dasyrhynchus talismani* has also been reported in the Pacific from *Carcharinus longimanus* (Heinz and Dailey 1974). All other reports describe plerocercoids from the vascular systems of teleost fishes (Bussieras and Aldrin 1965; Baudin Laurencin 1971; Chen and Yang 1973).

Prevalence of Infection by Host Species, Fish Size, and Season

A total of 53 skipjack tuna, 27 kawakawa, 10 bigeye tuna, and 470 yellowfin tuna were examined for the presence of parasites. We found only yellowfin tuna to be infected.

Infection in yellowfin tuna varied with size class. We found a significantly lower incidence of dorsal aorta infection in large fish. Of 220 individuals weighing 0.21 to 2.7 kg, 48% were infected, while of 250 fish weighing more than 45 kg, only 5.2% carried the parasite in their dorsal aortas. Viscera of a small subsample (N = 8) of the larger fish were examined and indicated that in larger fish the parasite infects (in the order of prevalence) the major arteries of the spleen, intestinal caeca, liver, mesenteries, and lateral blood vessels. Fish in intermediate size classes were not available for this study. Fish >3 kg do not survive the trip from the fishing grounds to the Kewalo Research Facility and are therefore not normally captured by commercial fishermen for return to the laboratory. Fish <45 kg are not common at the Honolulu Fish Auction where they could be examined during normal processing. The

purchase of intermediate-sized yellowfin tuna specifically for this study (yellowfin tuna intended for market cannot be necropsied and then sold) was prohibitively expensive.

Infection of yellowfin tuna appears to vary seasonally. Figure 1 shows changes in prevalence of dorsal aorta infection in small (<3 kg) yellowfin tuna captured between February 1985 through March 1986. Prevalence remained stable for approximately 6 months during the winter through early summer. Then in late summer of 1985, prevalence dropped dramatically from 66 to 11%. Beginning in October 1985, prevalence increased steadily, reaching 39% in February-March 1986, the last months for which data are available.

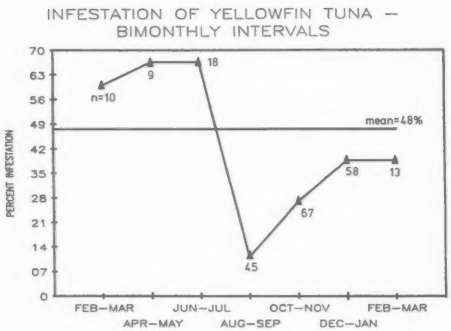

FIGURE 1.—Prevalence (percent infection) of the dorsal aorta by the plerocercoid stage of the cestode *Dasyrhynchus talismani* in small (0.3-3 kg) yellowfin tuna caught near the Hawaiian Islands from February 1985 to March 1986.

Pathology

In infected fish, the anterior dorsal aorta was partially to nearly completely occluded by a parasitic embolus which contained one to several larval cestodes. Figure 2a shows this vessel in a moderately infected yellowfin tuna. Parasites and a small amount of host inflammation are evident in the anterior end (to the right). A normal portion of vessel, with a smooth wall, is seen to the left. Figure 2b shows the anterior dorsal aorta from a very heavily infected fish.

Histological examination revealed that parasitic emboli were primarily composed of larval cestodes, mononuclear cells with eosinophilic granules (presumed to be eosinophils), epitheloid cells (histocytes), fibroblasts, and collagen fibers (Fig. 3). Larval cestodes within the dorsal aorta were associated with a chronic severe endarteritis and, to a lesser extent, mesoarteritis. In heavily infected fish, collapsed channels were commonly found within emboli. Undoubtedly these channels expanded in life with increases in intraluminal blood pressure to allow blood to flow through the vessel. Necrotic worms were also seen, suggesting that the host's defense system was at least partially capable of killing the larvae located in the dorsal aorta.

Infection of other arteries was usually by one, or at most two, larger parasites which were never seen to be folded. These parasites had a bulbous anterior end which always pointed downstream. No evidence of host immune response was observed when the parasites were in vessels other than the dorsal aorta.

Effect of Infection on Measures of Physiological Fitness

Mean (±1 SD) relative condition factor and mean (±1 SD) relative organ weight data are given in Table 1 for the fish sampled between May 1985 and September 1986. Table 2 lists the same parameters plus mean relative otolith weight, and mean RNA/DNA ratio for fish sampled from the single school captured on 15 January 1986. Means were compared with Student's two-tailed T test, with $P = 0.05$ taken as the minimum level for statistical significance.

Examination of data from all the fish caught May 1985-September 1986 reveals statistically significant differences in relative liver and heart weights for parasitized and unparasitized fish. On the average, parasitized fish, have 15% smaller livers, and 9% *smaller* hearts than unparasitized fish. Relative condition factors were not significantly different. When data from fish coming from the single school are examined, there are no statistically significant differences in these three parameters, relative otolith weight, or in RNA/

TABLE 1.—Relative condition factor, relative liver weight, and relative heart weight, of yellowfin tuna sampled between May 1985 and September 1986.

Fish	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight
Uninfected	1.00 (±0.10) $N = 109$	1.02 (±0.22) $N = 82$	1.01 (±0.18) $N = 88$
Infected	0.976 (±0.057) $N = 35$	0.867 (±0.098)* $N = 22$	0.919 (±0.085)* $N = 32$

*Uninfected and infected groups different at $P = 0.05$ level.

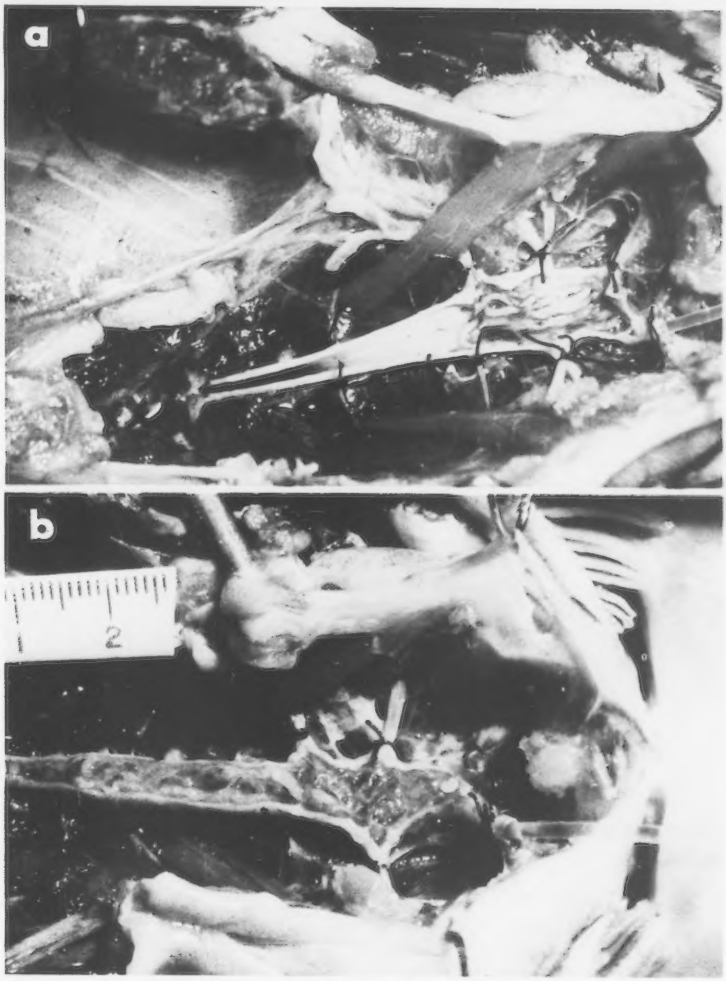

FIGURE 2a.—The anterior dorsal aorta of a moderately infected yellowfin tuna. In the anterior end of the vessel (to the right) are parasites and host inflammation.

FIGURE 2b.—The anterior dorsal aorta of a heavily infected yellowfin tuna. The vessel's lumen is all but occluded by parasites and host inflammation. Ruler divisions are in mm.

TABLE 2.—Relative condition factor, relative liver weight, relative heart weight, relative otolith weight, and RNA/DNA ratio of yellowfin tuna sampled 15 January 1986.

Fish	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight	Mean (±SD) relative otolith weight	Mean (±SD) RNA/DNA ratios
Uninfected	1.00 (±0.04) $N = 23$	1.00 (±0.08) $N = 23$	1.00 (±0.06) $N = 23$	1.00 (±0.04) $N = 12$	28.9 (±8.9) $N = 21$
Infected	0.995 (±0.035) $N = 12$	1.00 (±0.07) $N = 12$	0.975 (±0.074) $N = 12$	0.980 (±0.058) $N = 8$	33.1 (±11.1) $N = 10$

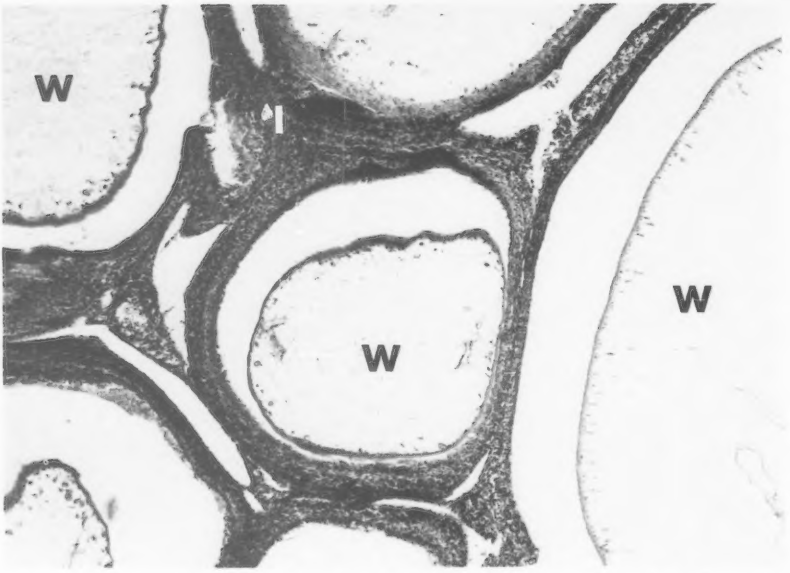

FIGURE 3.—Photomicrograph of a cross section of the dorsal aorta containing parasites and host inflammation of a heavily infected yellowfin tuna. The host inflammation (I) and cross sections of the parasites (W) can be easily differentiated. Hematoxylin and eosin stain.

DNA ratios. RNA/DNA ratios were compared directly (rather than by calculating relative RNA/DNA ratios) because they were found not to be correlated with body weight (correlation coefficient = 0.04).

Data from *unparasitized* fish collected in August and September 1985 were analyzed separately from all remaining *unparasitized* fish. This was done because we found dramatically lower rates of infection (11%) during those 2 months than during the preceding 2 months (67% infected) and assumed this to be due to an influx of a new group of small yellowfin tuna into the Hawaiian fishery. New regression parameters for body weight on fork length, heart weight on body weight, and liver weight on body weight were calculated using data from unparasitized fish excluding those caught during August-September 1985. Mean relative condition factors and relative organ weights were then recalculated.

Table 3 shows mean relative condition factors, mean relative liver weights, and mean relative heart weights for unparasitized fish captured during August and September 1985, unparasitized

TABLE 3.—Relative condition factor, relative liver weight, and relative heart weight from uninfected yellowfin tuna sampled during August and September 1985, from all other uninfected yellowfin tuna, and all infected fish.

Group	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight
August-September 1985 uninfected fish	1.11 (±0.08)* $N = 36$	1.24 (±0.28)* $N = 35$	1.22 (±0.18)* $N = 36$
All other uninfected fish	1.00 (±0.09) $N = 73$	1.01 (±0.17) $N = 47$	1.00 (±0.09) $N = 52$
Infected fish	1.01 (±0.06) $N = 35$	0.937 (±0.102) $N = 22$	1.00 (±0.09) $N = 32$

*Uninfected groups different at $P = 0.01$ level.

fish captured at all other times of the year, and all parasitized fish, based on the new regression parameters. The two groups of *unparasitized* fish show statistically significant differences in all three. Fish caught during August and September were on the average 11% heavier at a given body size (i.e., relative condition factor = 1.11), had livers an average of 23% heavier, and had hearts an average of 22% heavier than those unparasitized fish captured at other times of the year. When unparasitized fish, excluding those caught during August and September, are compared with parasitized fish, there are now no statistically significant differences in mean relative condition factors, mean relative liver weights, or mean relative heart weights. The data from unparasitized fish captured in August and September, when included in the complete data set, are therefore responsible for the observed differences in relative heart and liver weights between infected and uninfected fish seen in Table 1.

In Vitro Perfusion of the Dorsal Aorta

Three parasitized and five unparasitized fish, ranging in weight from 0.915 to 2.666 kg, were used in this series of experiments. The intensity of infection was subjectively classified as slight, moderate, or heavy. Perfusion pressures were normalized to a 1 kg fish weight by dividing the observed pressures by the reciprocal of body weight, in kilograms. Moderately and heavily infected fish showed higher perfusion pressures at a given flow rate than did unparasitized animals (Fig. 4). While no data are available on the normal cardiac outputs and blood pressures in swimming yellowfin tuna, restrained and lightly anesthetized yellowfin tuna have cardiac outputs of approximately 40-60 mL/kg and dorsal aorta blood pressures of 50-70 mm Hg (D. R. Jones and R. W. Brill, unpubl. obs.). Figure 4 shows that at normal cardiac outputs, the apparent occlusion of the dorsal aorta caused by the parasites and host inflammation is indeed real and should cause moderately and heavily infected fish to have excessively high blood pressures, high cardiac energy demands and presumably reduced fitness.

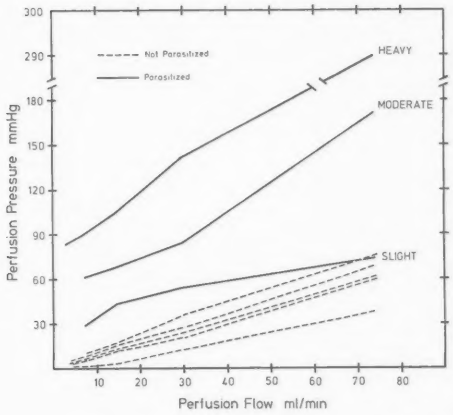

FIGURE 4.—In vitro pressure required to pump various rates of saline down the dorsal aorta of parasitized and unparasitized yellowfin tuna. The fish ranged in size from 0.915 to 2.666 kg. Data have been normalized to a body weight of 1 kg.

DISCUSSION

Prevalence of Infection by Species, Size, and Season

Our data indicate that in Hawaiian waters *D. talismani* is limited to yellowfin tuna. However, *D. talismani* has been reported to occur in Atlantic bigeye tuna (Bussieras and Aldrin 1965). Since we examined relatively few individuals of this species, we cannot rule out the occurrence of this parasite in bigeye tuna in the central Pacific.

Skipjack tuna, bigeye tuna, kawakawa, and yellowfin tuna often occur simultaneously in the same areas and show a great overlap in prey species (King and Ikehara 1956; Waldron and King 1963). It is therefore unlikely that host specificity is attributable to only yellowfin tuna ingesting the intermediate host, which is not known but is most likely a small crustacean (Deardorff et al. 1984). Host specificity could arise if the procercoid of *D. talismani* is not stimulated or is unable to penetrate the gut wall of tuna species other than yellowfin tuna, or that species of tuna other than yellowfin are capable of immune rejection (Orr et al. 1969).

The reasons for the dramatic decrease in incidence of dorsal aorta infection in large (>45 kg) yellowfin tuna are unknown. Possible reasons include procercoids ingested less frequently by larger animals, host destruction of the parasite, increased mortality of parasitized fish, or movement of the parasite out of the dorsal aorta into other major arterial vessels. Of these alternatives, increased mortality of infected fish seems unlikely.

While we did not demonstrate directly the pre-

ence of antibodies against the parasite, several histological cross sections show worms in stages of degeneration, and host destruction of larval and adult cestodes has been shown in other teleosts (Kennedy and Walker 1969; Smith 1973; MacKenzie 1975). Examination of a small number of pyloric caeca, liver, spleen, lateral arteries, and stomach vasculature of large yellowfin tuna (>45 kg) showed >85% infection, suggesting 1) that the parasite may move out of the dorsal aorta into other large arteries as yellowfin tuna grow, 2) that the host response to the parasite may be less vigorous in vessels other than the dorsal aorta, and/or 3) that the parasite may preferentially select other vessels in larger fish. Baudin Laurencin (1971) found a decrease in branchial artery infection of yellowfin tuna with increasing body size, but no change in rates of infection of abdominal vessels.

The change in the rate of infection seen in August and September 1985 in small yellowfin tuna (Fig. 1) is, we believe, due to a large influx of uninfected fish into the Hawaiian fishery. Although we have no direct corroborating evidence, such as increased catch per unit effort for this size yellowfin tuna at that time, Tester and Nakamura (1957) have shown that there are repeated influxes of small yellowfin tuna into areas near the main Hawaiian Islands during late summer and early fall. Furthermore, the dramatic differences seen in relative condition factors, relative liver weights, and relative heart weights between unparasitized fish caught during August-September 1985, and the remaining unparasitized fish, clearly imply that the former group had a different history.

We have no evidence nor are we hypothesizing that these groups come from genetically isolated subpopulations. We do believe, however, that the two groups were separate most likely since hatching. We do not know the maximum lifespan of the dorsal aorta parasite, but one yellowfin tuna killed after 172 days in captivity at the Kewalo Research Facility was parasitized. Since fish in captivity are fed only frozen food and their tanks are supplied with filtered seawater (Queenth and Brill[5]), it is unlikely this fish became infected after capture. Yellowfin tuna of the 1-3 kg size range are about 270-360 days old (Uchiyama and Struhsaker 1981) and therefore could have carried the parasite most of their lives.

The slow increase in prevalence from October 1985 through March 1986 remains to be explained, but could be due to emigration of the new group of yellowfin tuna out of the Hawaiian fishery or slowly increasing infection of the new group. This latter explanation implies higher prevalence of the parasite around islands which could be due either to a greater number of final (shark) or intermediate hosts around islands.

Pathology

The severe enarteritis associated with *D. talismani* infection suggests that the parasite is recognized by the fish's defense system as foreign material in the dorsal aorta. Dead worms within the inflammatory tissue imply that the parasite is not well adapted for survival in this location. Presumably, *D. talismani* would elicit, and be attacked by, a similar inflammatory response irrespective of its location within the vasculature. This response was not observed in other vessels and additional work is needed to clarify the site specificity of the immune response. Our findings also suggest that cellular elements are responsible for the destruction of the larval cestodes when located in the dorsal aorta.

Effect of the Infection of the Dorsal Aorta on Natural Mortality

We found no evidence to support our original hypothesis that infected yellowfin tuna are activity limited and therefore less able to secure food. When the data from the unparasitized fish caught August-September 1985 are excluded, there are no differences in relative condition factors, relative liver weights, or relative heart weights between parasitized and unparasitized fish. When parasitized and unparasitized fish from the single school caught 15 January 1985 are compared, no significant differences in these parameters, mean short-term (i.e., RNA/DNA ratios), or mean long-term (i.e., relative otolith weights) growth are evident.

Because parasite emboli appear to cause almost complete occlusion of the anterior dorsal aorta (the only blood vessel supplying the viscera and swimming muscles), the lack of differences between infected and uninfected fish was not expected. Overstreet (1977), investigating the effects of plerocercoid infection on sciaenid fishes in

[5]Queenth, M. K. K., and R. W. Brill. 1983. Operations and procedures manual for visiting scientists at the Kewalo Research Facility. Southwest Fish. Cent. Admin. Rep. H-83-7, 16 p. Natl. Mar. Fish. Serv., NOAA, Honolulu, HI.

the Gulf of Mexico, found no apparent detrimental effect on the host, but these parasites were found encysted in the muscle, not the vasculature. Although the ability of parasitized yellowfin tuna to function as predators are apparently not affected, their ability to escape predation remains to be tested. It is possible that infected yellowfin tuna are subjected to differential predation, as has been shown to be for roach, *Rutilus rutilus*, infected in the coelomic cavity by the plerocercoid of *Ligula* sp. (Van Dobben 1952).

Pressure Flow Relationships in the Dorsal Aorta

The unphysiologically high pressures required to pump saline through the dorsal aortas of moderately and heavily infected fish remain to be explained in light of apparent lack of effects of the parasite on other measures of the fish's condition, including the absence of cardiac hypertrophy. It is possible that the dorsal aorta, because of its thick muscular wall (J. Brock, unpubl. obs.), becomes significantly less compliant postmortem. Such changes could require that higher pressures be generated to create a given degree of expansion. Therefore higher pressures would be required postmortum to push a given flow rate of saline through the vessel.

In summary, *D. talismani* appears to have no significant adverse effects on the physiological fitness and natural mortality of small yellowfin tuna in spite of apparent vascular blockage. How these fish are able to cope with dorsal aorta infection requires further investigation.

Use of *Dasyrhynchus talismani* as a Natural Tag for Tracing Movements of Small Yellowfin Tuna

We feel that this parasite offers excellent potential as a natural marker for tracking the movements of separate groups of small yellowfin tuna between or into specific fisheries. (For a review of the use of parasites to delineate stocks for management purposes, see MacKenzie 1983.) *Dasyrhynchus talismani* does not fulfill all seven requirements for an ideal natural tag listed by Sindermann (1983), but it does appear to meet the requirements of 1) having significant differences of geographic prevalence, 2) being easily detected, 3) being able to be definitively identified, 4) having minimum effect on host survival, and 5) surviving in the host for long periods. Data on prevalence of *D. talismani* could be combined with data on prevalence of other parasites, as has been shown by Lester et al. (1985) for skipjack tuna, or combined with data on relative condition factor, relative heart weight, and relative liver weight to provide information on fish movements.

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AGE AND GROWTH OF SPANISH MACKEREL, *SCOMBEROMORUS MACULATUS*, FROM FLORIDA AND THE GULF OF MEXICO

WILLIAM A. FABLE, JR., ALLYN G. JOHNSON, AND LYMAN E. BARGER[1]

ABSTRACT

Otoliths from 1,787 Spanish mackerel, *Scomberomorus maculatus*, were used to estimate age and growth rates of this species from Florida and the Gulf of Mexico. There was a wide range of lengths within an age group: the oldest male was 7 years old, while the oldest female was 9 years old. Length at age was significantly different for sexes, sampling areas, and collection gear. The von Bertalanffy growth equations were as follows: males (all areas combined) $l_t = 794\ (1 - e^{-0.24(t + 0.94)})$; females (all areas combined) $l_t = 739\ (1 - e^{-0.33(t + 0.99)})$; males (Florida only) $l_t = 776\ (1 - e^{-0.27(t + 0.73)})$; females (Florida only) $l_t = 731\ (1 - e^{-0.38(t + 0.73)})$, where l = fork length (mm) and t = years.

Spanish mackerel, *Scomberomorus maculatus*, are found in the western Atlantic Ocean from the Gulf of Maine to the Yucatan Peninsula (Collette et al. 1978), and have their center of abundance off Florida (Trent and Anthony 1978). They support extensive commercial and recreational fisheries in the U.S. south Atlantic and Gulf of Mexico. In 1985, U.S. commercial landings totaled 5.8 million pounds (2,631 t) (U.S. Department of Commerce 1986a) while recreational landings were estimated to be 2.1 million pounds (953 t) (U.S. Department of Commerce 1986b). Information on Spanish mackerel published prior to 1978 actually concerned two species, *S. maculatus* and *S. brasiliensis* (Collette et al. 1978). Collette et al. (1978) determined that Spanish mackerel south of the Yucatan Peninsula (on the Central and South American Atlantic coasts) are *S. brasiliensis*, and those along U.S. coasts are *S. maculatus*.

There is disagreement in the literature on the interpretation of annuli on otoliths of Spanish mackerel. The first information on age and growth of *S. maculatus* was from fish collected in southeast Florida (Klima 1959). Later, Mendoza (1968) gave some limited age and growth information on *S. maculatus* from Veracruz, Mexico, and Powell (1975) provided the most recent information on Spanish mackerel age, growth, and reproduction in Florida. Powell interpreted annuli on Spanish mackerel otoliths differently than did Klima, and the different age determinations yielded different growth estimates. Mendoza (1968) did not estimate growth except by presenting his data in tabular form.

We undertook this investigation to resolve these uncertainties in the literature and to derive more current age and growth parameters. This information will provide a better basis for rational management of this species.

STUDY AREA AND METHODS

We collected 1,929 Spanish mackerel from 1977 through 1981 from the south Atlantic and Gulf of Mexico coasts of the United States. Most (1,422) of the fish came from northwest Florida and only 10 came from north of south Florida on the Atlantic coast (Table 1). Fork length (FL) of each

TABLE 1.—Numbers of Spanish mackerel collected for age and growth study.

Area	Year					Total
	1977	1978	1979	1980	1981	
Texas	—	48	—	—	—	48
Mississippi/ Louisiana	41	79	—	23	—	143
Northwest Florida	59	377	31	955	—	1,422
South Florida	—	87	31	59	129	306
Georgia	—	10	—	—	—	10
Total	100	601	62	1,037	129	1,929

[1]Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, 3500 Delwood Beach Road, Panama City, FL 32407-7499.

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mackerel was measured to the nearest millimeter. Sagittal otoliths were removed, washed, and stored dry. The clearest, most legible otolith from each fish (based on visual observation) was examined to estimate age and growth.

Whole otoliths were placed in a black-bottomed watch glass containing 100% glycerin and examined with a binocular microscope at 28× using reflected light. Otolith radius (OR) was measured in ocular micrometer units (1 unit = 0.0363 mm) on the posterior surface from the focus to the distal margin along the axis of the sulcus acousticus (Powell 1975). Growth marks were counted and measured from the focus along the radius to their distal edge. The marks were opaque (light) under reflected light, while the interspaces were hyaline or translucent (dark).

Otoliths were classified into age groups based on the number of opaque nonmarginal marks (Powell 1975). A mark was considered complete when a hyaline (dark) interspace or margin was visible from successive growth. Three readers independently examined each of 520 otoliths to test the precision of our ageing technique. This information was analyzed using the method of Beamish and Fournier (1981). All other otoliths were independently examined by two readers; if their results did not agree, the data were not used.

To compare age estimates based on surface (whole) and internal (sectional) examination, we sectioned 70 otoliths which had been previously examined on the surface (2-10 otoliths from different fish from each age 0+ through 8+), following the methods of Johnson et al. (1983).

We determined time of annulus formation and validated our ageing technique by comparing monthly percentage frequencies of otoliths with opaque margins. A high percentage frequency (>45%) indicated recent annulus formation. We used a chi-square test to compare the monthly frequencies.

The relationship between otolith radius and fork length was determined and used to back calculate fork lengths at earlier ages (Tesch 1971; Ricker 1975; Everhart et al. 1975). We used analysis of covariance (ANCOVA) with age as the covariate to test for differences in growth rates (lengths at age) of fish collected in different locations, by different gears, and of different sexes. Mean back-calculated lengths were used to calculate von Bertalanffy (1938) growth parameters, employing a computer program developed by Abramson (1971).

RESULTS AND DISCUSSION

Validation

Age validation has often been overlooked in the age and growth literature (Beamish and McFarlane 1983). Although there are numerous methods available to establish the annual nature of otolith growth rings, we applied marginal increment analysis, because it was the only practical method to use on this migratory, pelagic species.

Annulus formation occurred in March, April, or May (Fig. 1). A chi-square test ($\chi^2 = 338.47$, $df = 1, P < 0.001$) showed a highly significant difference between the occurrence of otoliths with opaque margins in these months versus the other nine months of the year. Our findings are in agreement with Powell (1975) in that the main period of opaque mark formation was in the spring or early summer. He reported mark formation in May, June, and July by examination of marginal increments. Previously Klima (1959) described both summer and winter growth rings and evaluated the marginal condition to decide that marks were deposited annually. Our observations on the appearance of annuli in Spanish mackerel otoliths agreed with Powell (1975), in that we also were unable to discern the "first winter mark" that Klima (1959) described.

Age

To estimate the precision of our ageing, we compared sections to whole otoliths and evaluations by different readers. Examination of 70 sectioned otoliths provided a 97.4% agreement with previous surface examination of the same otoliths. Surface age determinations of three readers on 520 otoliths had a 97.7% agreement. Using the technique of Beamish and Fournier (1981), the index of average percent error was 0.3273, which we think is excellent.

Of 1,929 Spanish mackerel examined, 1,787 (92.6%), ranging from 148 to 802 mm FL, were aged. The oldest female was 9 years old, while the oldest male was 7 years old. Powell's (1975) oldest fish, a female, was 8 years old, while Klima's (1959) oldest males and females were both 6 years old. These data and the data presented in Tables 2 and 3 indicate that females live longer than males.

We found a wide range of lengths within an age group for both sexes (Tables 2, 3), as did Powell, with some Spanish mackerel of age 0 through 5 in

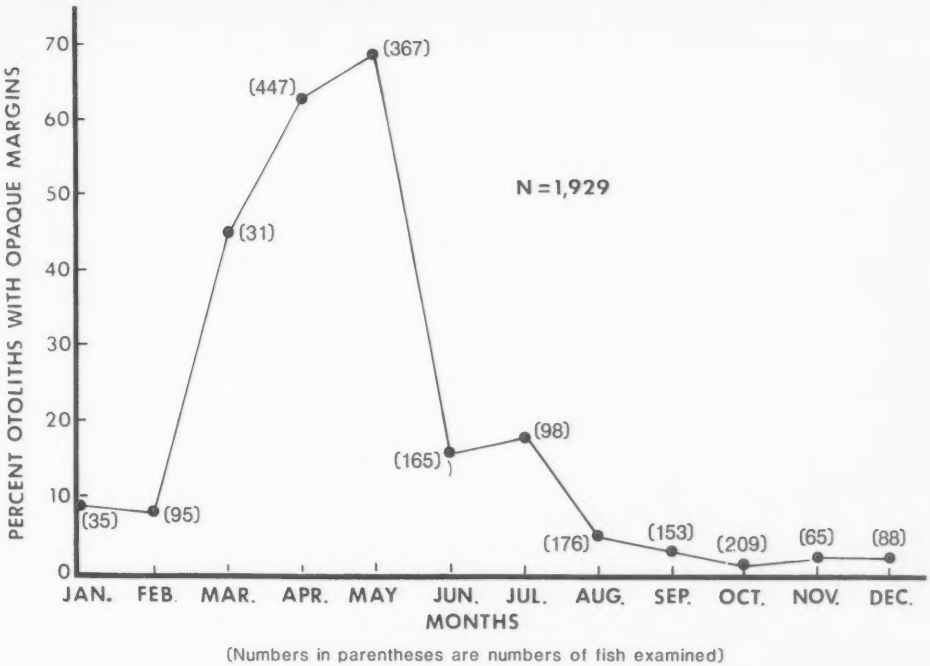

FIGURE 1.—Monthly percentage frequencies of Spanish mackerel otoliths with opaque margins.

the same size interval. In the closely related king mackerel, *S. cavalla*, Johnson et al. (1983) reported a similar situation. Our results substantiate wide variation in growth rates of individual Spanish mackerel.

Growth

Otolith radius (OR) was closely correlated with fish length (FL). The curvilinear relation $FL = 1.5091\ OR^{1.2639}$ ($r = 0.944$) had a slightly better fit than the linear equation $FL = -102.8061 + 6.1295\ OR$ ($r = 0.936$). We used the former equation to back calculate lengths at former ages for 949 fish that had at least one annulus (838 fish had no annuli and were classified as age 0). Neither Klima nor Powell reported any equations for an OR versus FL relationship.

The mean back-calculated annual increments of fork lengths for male and female Spanish mackerel from all areas and years combined (Tables 4, 5) indicate that growth rates were rapid until age 5 in females and to age 6 in males (the age 6 increment in males was based on one fish). After these ages, growth rates slowed appreciably. Early growth was more rapid in females than males (first annual increment 123.6 as compared to 98.7). However, males maintained a higher growth rate through age 6, except for age 5, when the female annual increment was 55.3 mm versus 47.9 mm in males.

Our back-calculations for Spanish mackerel showed variation in mean fork lengths at age between sexes, areas, and years (Table 6). Females from south Florida grew faster than any other group and males from there grew faster than any other males. For Spanish mackerel from northwest Florida, where the largest number of fish were collected, analysis of covariance (ANCOVA) indicated significant differences in growth (length-at-age) between sexes and collecting gears (Table 7).

ANCOVA was also used to test the significance of growth differences among geographic areas

TABLE 2.—Fork length (mm) composition, in percent, of male Spanish mackerel by age group (locations combined).

Length group	Age in years							Total number of fish
	0	1	2	3	4	5	7	
175-199	100.0							1
200-224	100.0							1
225-249	100.0							5
250-274	100.0							2
275-299	68.3	31.7						41
300-324	76.5	23.5						102
325-349	51.0	47.1	1.9					155
350-374	47.7	47.7	4.5					88
375-399	20.7	59.8	17.1	1.2				82
400-424	5.5	78.2	14.5					55
425-449	22.2	33.3	22.2	22.2				9
450-474	9.1	54.5	18.2		9.1	9.1		11
475-499		50.0			50.0			2
500-524		16.7	33.3	33.3	16.7			6
525-549		40.0	40.0	20.0				5
550-574			50.0			50.0		2
575-599				33.3	66.6			3
600-624								0
625-649						100.0		3
650-674								0
675-699							100.0	1
700-724						100.0		1
Total								575

TABLE 3.—Fork length (mm) composition, in percent, of female Spanish mackerel by age group (locations combined).

Length group	Age in years										Total number of fish
	0	1	2	3	4	5	6	7	8	9	
175-199	100.0										1
200-224	100.0										2
225-249	80.0	20.0									5
250-274	100.0										3
275-299	96.7	3.3									30
300-324	84.8	13.6	1.5								66
325-349	77.0	23.0									152
350-374	52.4	46.4	1.2								166
375-399	46.7	51.1	2.2								137
400-424	41.1	52.5	5.7	0.7							141
425-449	22.8	62.4	12.9	2.0							101
450-474	25.3	49.3	20.0	2.7	1.3		1.3				75
475-499	8.1	48.4	40.3	3.2							62
500-524	5.3	52.6	31.6	8.8		1.8					57
525-549	1.9	39.6	32.1	17.0	9.4						53
550-574		25.0	22.5	37.5	15.0						40
575-599		5.0	30.0	40.0	2.5						40
600-624		5.9	23.5	41.2	23.5	5.9					17
625-649			13.6	45.5	22.7	13.6	4.5				22
650-674			6.3	25.0	25.0	25.0	6.3	6.3	6.3		16
675-699				16.7	33.3	25.0	8.3	16.7			12
700-724						42.9	14.3		42.9		7
725-749				16.7		33.3		16.7	16.7	16.7	6
750-774											0
775-799							100.0				1
Total											1,212

TABLE 4.—Mean back-calculated fork lengths (mm) at age for male Spanish mackerel from all areas, 1977-81.

Age group	$\bar{X}$ FL at capture	N	Average back-calculated FL at age							
			1	2	3	4	5	6	7	
I	363.9	237	296.9							
II	413.7	33	306.4	382.2						
III	488.1	7	318.2	415.4	458.2					
IV	536.8	4	353.8	423.5	483.9	529.3				
V	605.0	5	374.9	448.2	522.4	567.1	596.3			
VI	—	0	—	—	—	—	—	—		
VII	679.0	1	342.0	521.8	570.9	606.5	642.5	657.1	671.7	
		287	300.8	399.5	489.8	556.1	604.0	657.1	671.7	Weighted mean
				98.7	90.3	66.3	47.9	53.1	14.3	Annual increment

TABLE 5.—Mean back-calculated fork lengths (mm) at age for female Spanish mackerel from all areas, 1977-81.

Age group	$\bar{X}$ FL at capture	N	Average back-calculated FL at age									
			1	2	3	4	5	6	7	8	9	
I	420.1	437	344.6									
II	503.6	113	340.8	463.1								
III	580.9	62	349.2	480.2	550.8							
IV	596.7	30	356.9	471.1	529.2	580.0						
V	682.0	11	359.9	471.0	565.1	625.4	666.6					
VI	683.0	3	405.1	472.9	546.5	602.5	643.7	673.7				
VII	654.7	3	324.1	431.8	485.4	529.2	572.3	617.3	645.7			
VIII	696.0	2	329.7	458.9	521.0	557.6	615.2	649.6	670.5	688.0		
IX	737.0	1	399.0	470.0	529.0	596.7	653.4	685.3	704.6	717.5	730.5	
		662	345.4	469.0	543.8	587.9	643.2	650.8	663.8	697.8	730.5	Weighted mean
				123.6	74.8	44.1	55.3	7.6	13.0	34.0	32.7	Annual increment

TABLE 6.—Weighted means of back-calculated fork lengths (mm) for male and female Spanish mackerel from all areas and years having appreciable numbers (over 100) of mackerels sampled.

Age group	All locations			Northwest Florida			Louisiana	South Florida		All Florida
	1978	1980	1981	1978	1980	All years	All years	1981	All years	All years
Males										
I	285	303	356	281	300	293	321	384	332	299
II	356	403	465	347	392	380	384	483	438	399
III	[1]448	474	531	[1]470	[1]460	[1]463	[1]440	558	508	494
IV		538	584		[1]529	[1]529	[1]479	607	566	561
V		[1]561	652		[1]561	[1]561	[1]454	[1]652	[1]654	[1]631
VI			[1]657					[1]657	[1]657	[1]657
VII			[1]672					[1]672	[1]672	[1]672
Females										
I	325	347	371	326	346	342	334	366	364	348
II	428	465	507	434	466	454	436	509	500	475
III	492	526	573	486	536	517	500	574	573	557
IV	[1]564	518	614	[1]555	[1]542	[1]548	518	615	614	607
V		[1]485	655				[1]536	655	654	654
VI		[1]540	665				[1]540	665	665	665
VII		[1]572	682				[1]572	682	682	682
VIII			[1]698					[1]698	[1]698	[1]693
IX			[1]730					[1]730	[1]730	[1]730

[1]Lengths based on less than 5 fish.

TABLE 7.—Results of analysis of covariance for growth differences observed in Spanish mackerel collected in northwest Florida, and fish collected in all areas by recreational hook and line, and gill net.

Source	Sum of squares	df	Mean square	*P*	Tail probability
Gill net					
Gear	2,499.15	2	1,249.57	13.04	0.00
Sex	5,275.31	1	5,275.31	55.03	0.00
Gear × sex	136.80	2	68.40	0.71	0.49
Age	41,384.91	1	41,384.91	431.73	0.00
Error	75,440.13	787	95.86		
n = 794					
NW Florida					
Area	3,792.09	2	1,896.05	22.83	0.00
Sex	476.13	1	476.13	5.73	0.02
Area × sex	689.00	2	344.50	4.15	0.02
Age	42,623.18	1	42,623.18	513.16	0.00
Error	38,955.39	469	83.06		
n = 476					
Recreational hook and line					
Area	1,132.44	2	566.22	5.42	0.00
Sex	2,673.83	1	2,673.83	25.59	0.00
Area × sex	183.17	2	91.58	0.88	0.42
Age	124,338.42	1	124,338.42	1,190.00	0.00
Error	78,886.76	755	104.49		
n = 762					

(sex, area × sex, and age were also included in the covariance model) for recreational hook and line samples and gill net samples. Area differences were highly significant for both gear types, and sex differences were highly significant for gill net-caught fish, but somewhat less so for hook and line samples (Table 7). The area × sex interaction was significant for hook and line, but not gill net samples.

These ANCOVA results demonstrate that females grew significantly faster than males. The significant differences between sampling gears are no doubt due to gear selectivity, i.e., hook and line selecting for larger fish of a given age and gill nets selecting for a specific size fish. Significant differences between sampling areas (consistent for both sampling gears) substantiate faster growth in south Florida (fish were larger at a given age) than in northwest Florida or Louisiana.

We compared back-calculated lengths-at-age of Spanish mackerel (from all areas and from Florida alone) with those of Powell (1975); lengths at ages 1 and 2 for both sexes were shorter, while those for ages 3-5 were increasingly longer (Table 8). There was a greater discrepancy between our data and Powell's for males than for females. Florida males from our study were 38 mm shorter than Powell's at age 1, but by age 5 they were 120 mm longer. Florida females from our study were 25 mm shorter than Powell's at age 1, but by age 5 they were 33 mm longer. Some of this discrepancy can be explained by the fact that Powell used the direct proportion method for his back-calculations, whereas the program by Abramson (1971) employs the regression method. Carlander (1981) pointed out potential problems with this method, but they primarily concern the fact that when using the scales for ageing, not all scales on a fish are the same size. This problem is of lesser importance when ageing is done from otoliths.

TABLE 8.—Mean back-calculated fork lengths (mm) at age by sex for Spanish mackerel from Powell (1975) and this study. Powell's data were transformed from standard length by his formula FL = 1.0728 SL + 2.4267.

Age group	Powell		Fable et al.			
			Florida		All areas	
	Males	Females	Males	Females	Males	Females
I	337	373	299	348	301	345
II	421	481	399	475	400	469
III	459	542	494	557	490	544
IV	489	580	561	607	556	588
V	511	621	631	654	604	643
VI			657	665	657	651
VII			672	682	672	664
VIII				698		698
IX				730		731

Our estimates of the von Bertalanffy growth coefficient (k) are smaller, and our asymptotic

lengths (L_∞) are larger (especially for males) than those derived by Powell (1975) and Nomura (1967) (Table 9). Nomura used Klima's (1959) data to compute growth curves for Florida fish. Our L_∞ estimates are much closer to the maximum observed lengths in our samples (802 mm FL female and 723 mm FL male) than were the estimates from other authors. The differences between our estimates and Powell's (1975) are easily explained because we included the oldest fish in our back-calculations, whereas Powell only included fish up to 5 years old, forcing his growth coefficient (k) to be higher. Therefore, we believe our growth parameters are a more accurate reflection of population growth and more appropriate to use in assessment of the status of the stock.

TABLE 9.—Von Bertalanffy growth parameters for Spanish mackerel.

Author	Males			Females		
	K	L_∞ (FL mm)	t_0 (years)	K	L_∞ (FL mm)	t_0 (years)
Fable et al. all areas combined	0.24	794	−0.94	0.33	739	−0.99
Fable et al. Florida	0.27	776	−0.73	0.38	731	−0.73
Powell (1975)	0.48	555	−1.12	0.45	694	−0.78
Nomura (1967) using Klima's (1959) data	0.40	607	+0.15	0.40	720	+0.28

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FEEDING HABITATS OF SPOT, *LEIOSTOMUS XANTHURUS*, IN POLYHALINE VERSUS MESO-OLIGOHALINE TIDAL CREEKS AND SHOALS[1]

STEVEN P. O'NEIL[2] AND MICHAEL P. WEINSTEIN[3]

ABSTRACT

Young-of-year spot, *Leiostomus xanthurus*, were collected by otter trawl within tidal creeks and on adjacent shoals in polyhaline and meso-oligohaline zones of the York River, Virginia. Total densities of spot at Blevins Creek, a polyhaline system, were twice that of the meso-oligohaline Goalders Creek.

Stomach content analysis confirmed previous studies of the generally opportunistic feeding strategy of juvenile spot. However, distinct differences in food utilization were observed between creeks and among creek and shoal stations. In addition, prey utilization differences due to habitat generally paralleled seasonal distribution patterns of dominant macrobenthos reported for the area.

Two major ontogenetic groups were distinguished. Small spot (<30 mm SL) consumed more planktonic food items (calanoid copepods) than the larger size classes, which fed on more benthic prey and displayed greater overlap in diet. Small spot tended to be selective; larger spot were more opportunistic.

Tidal salt marshes and their associated drainages are recognized primary nurseries for spot, *Leiostomus xanthurus*, (Herke 1971; Parker 1971; Weinstein 1979; Currin et al. 1984). Shortly after recruitment, young spot tend to concentrate in tidal creeks, and by late spring densities in these creeks are often several times higher than in nearby seagrass habitats or shoal areas (Weinstein and Brooks 1983; Smith et al. 1984). Once recruited to tidal creeks, spot seem to take up residence, with limited movement out of (or between) marshes until the fall mass exodus (Weinstein 1983; Weinstein and Brooks 1983; Currin et al. 1984; Weinstein et al. 1984; Weinstein and O'Neil 1986).

The role of marsh nurseries as predation refuges versus feeding areas is currently under debate (Boesch and Turner 1984). As suggested by the studies of Vince et al. (1976), it is likely that the marsh serves in both capacities. Qualitative and quantitative data on food availability and quality and on differences among habitats will be necessary to resolve the food versus refuge question. Ultimately, these data should be supported by experimental studies on growth rates versus the quality of food resources in different habitats (Weisberg and Lotrich 1982). We report here on one of the steps in the process, a descriptive comparison of gut contents of spot collected in tidal creeks and shoal areas in marshes of two salinity regimes, meso-oligohaline and polyhaline.

Although the food habits of spot have been previously studied, most investigators captured spot in openwater habitats, not in the primary nurseries (Parker 1971; Stickney et al. 1975; Chao and Musick 1977; Sheridan 1979). Only Hodson et al. (1981) studied food utilization of spot in tidal creeks. Their population, however, was restricted mainly to small fish (<40 mm) capable of exploiting the small creek rivulets and susceptible to capture by block net. This study expands the effort of Hodson et al. (1981), and includes the entire seasonal residency period for spot in tidal creeks of the York River estuary, VA. A survey of food utilization was conducted in 1983 for all young-of-year size classes occupying two tidal creeks and nearby river shoals at widely separated salinities. Specific objectives of this effort were to 1) describe food utilization of juvenile spot in each habitat, 2) document any sequential ontogenetic changes in food utilization, and 3) compare the overall food utilization of spot residing in tidal creeks or adjacent shoals dissimilar in salinity. It was anticipated that feeding differences would reflect the availability and types of food in

[1]Virginia Institute of Marine Science Contribution No. 1419.
[2]Virginia Institute of Marine Science, Gloucester Point, VA 23062.
[3]Virginia Institute of Marine Science, Gloucester Point, VA 23062; present address: Lawler, Matusky & Skelly Engineers, One Blue Hill Plaza, Pearl River, NY 10965.

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the two salinity regimes and microhabitats constituting the creek and shoal sites.

STUDY AREA AND METHODS

The York River estuary, a subestuary of the Virginia portion of the Chesapeake Bay (Fig. 1), covers about 208 km^2 and extends 46 km from Tue Marsh Light to West Point, where it is formed by the confluence of the Pamunkey and Mattaponi Rivers. At two localities within the estuary, tidal creeks similar in physical dimensions (O'Neil 1983), but differing in salinity regimes, were selected as study sites: Goalders Creek, a meso-oligohaline site (sensu Remane 1934 and the Venice System of classification), and Blevins Creek, a polyhaline creek in the Guinea Marshes near the mouth of the river (Fig. 1).

Field Methods

Within each locality three stations were established: 1) in each creek approximately 1,500-2,000 m upstream (where trawling was still possible), 2) immediately inside the creek mouth, and 3) at shoal stations positioned approximately 200 m offshore in the York River proper in approximately 3 m of water.

Monthly collections (March-October 1982) with a 4.9 m semiballoon otter trawl with wings and body of 19 mm mesh and a 6.3 mm mesh cod end liner were made during daylight hours as close to high tide as possible. Four 2-min tows at about 1 m s^{-1} were made at each station.

To reduce the chances of regurgitation, specimens were initially anesthetized in a mixture of seawater and 0.02 mL quinaldine (mixed in 10 mL acetone). Buffered formalin (10%) was then added for preservation. The abdominal cavities of large fish (>80 mm) were pierced to allow sufficient preservation of food items in the stomach. Water temperature and salinity were recorded prior to trawling at each station.

Laboratory Methods

In the laboratory, spot from each collection were sorted and counted. Individual standard lengths (SL) were measured; when more than 50 spot were captured in a single collection, a random subsample of 30 fish was used for length measurements.

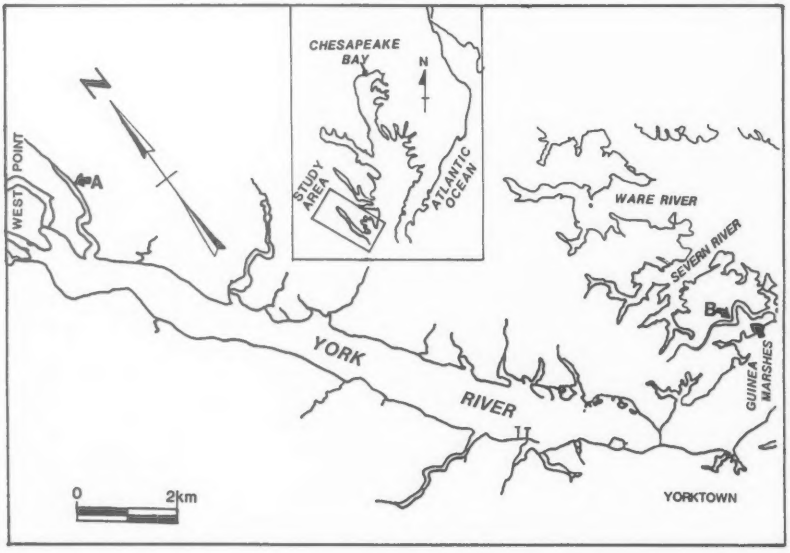

FIGURE 1.—York River, VA, and relative locations of tidal creeks examined. A = Goalders Creek, B = Blevins Creek.

For gut content analysis, fish from each of the four trawl samples representing a given station were pooled and then divided into several size classes. Initially, 5 mm size increments were used in order to corroborate the findings of others concerning an ontongenetic shift in feeding habits of spot. When mean standard lengths exceeded 20 mm, 10 mm size classes were adopted.

Initially, up to 20 stomachs were removed from randomly selected individuals in each size class. Later, based on prey item diversity (Hurtubia 1973) comparisons for the June samples, 12 stomachs per size class was set as the upper limit (O'Neil 1983).

Stomach contents were pooled within size classes and analyzed using the Carr and Adams (1972) sieve fraction technique. After washing stomach contents from each sieve (2, 0.85, 0.425, 0.25, 0.15, and 0.075 mm meshes) into a small fingerbowl, a random subsample of approximately 5 mL was removed. The subsample was placed in a labeled vial and the remainder was filtered onto a preweighed 55 mm filter pad and dried for 24 hours at 60°C. On the assumption that food particles of roughly the same size have approximately the same weight (Carr and Adams 1972), the total dry weight for each sieve fraction was proportioned among the prey types identified from its subsample. The Carr and Adams technique provided for rapid, accurate identification of food items from a large number of stomachs and has been used successfully by several investigators (Sheridan 1979; Stoner 1980; Livingston 1982; Lucas 1982).

Statistical Analysis

Dietary differences among various ontogenetic groups, between creeks, between stations within creeks, or for each month examined were compared using "normal" classification methods (Clifford and Stephenson 1975). Overlap of prey utilization was then determined using the complement of the Bray-Curtis dissimilarity measure:

$$\frac{\sum_{1}^{n} |x_{1_j} - x_{2_j}|}{\sum_{1}^{n} (x_{1_j} + x_{2_j})}$$

where n is the number of attributes (prey) and x_{1_j} and x_{2_j} are the values of the jth attribute for any pair of entities (size, station, month).

Separate matrices were constructed for each comparison from untransformed, pooled monthly data using COMPAH (Boesch 1977). The data in each matrix were then clustered by the group-average method (Lance and Williams 1967). Diet information was based on dry weights of the 30 prey taxa categories, all of which were mutually exclusive except for the unidentified (UID) and miscellaneous (MISC) categories (Table 1). Prey items contributing <0.1 mg of total dry weight per size class were eliminated prior to the analysis. The miscellaneous category contains the total of all food items individually representing <2% of the final dry weight.

In addition to the clustering procedure, reciprocal averaging ordination (Guinochet 1973; Hill 1973) was used to provide independent verifica-

TABLE 1.—Prey categories used for tropic comparisons. All but unidentified (UID) and miscellaneous (MISC) are mutually exclusive feeding categories.

AMP	Amphipoda
BIV	Bivalves
BRA	Branchipoda
CAL	Calanoids
CAP	Caprellidae
CLS	Clam siphons
CHI	Chironomidae
CHL	Chlorophyta
COR	Corophiidae
Crs	*Crangon septemspinosa*
CRZ	Crab zoea
Cs	*Callinectes sapidus*
CYA	Cyathura
DET	Detritus
Eh	*Eteone heteropoda*
Et	*Edotea tribola*
FOR	Foraminifera
GAM	Gammaridae
HA_1	Harpacticoid 1
HA_2	Harpacticoid 2
La	*Leucon americanus*
Lp	*Leptocheirus plumulosus*
MAC	*Macoma* sp
MAL	Maldanidae
Me	*Monoculodes edwardsi*
MISC	Miscellaneous
Na	*Neomysis americana*
NEM	Nematoda
NER	Nereidae
OLI	Oligochaeta
OST	Ostracods
PAL	Palaemonidae
PI	*Polydora ligni*
PLA	Plant matter
POL	Polychaeta
SPI	Spionidae
TEL	Teleosteii
UID	Unidentified remains
XAN	Xanthidae

tion of the dendrogram results. Reciprocal averaging is an eigenanalysis that ordinates both food type and habitat (or size class) variables simultaneously and defines axes such that the variance of the scores on each axis is maximized. The first axis, therefore, represents the path of maximum variance, the second axis the next greatest, and so forth. This analysis was performed with ORDIFLEX (Gauch 1977).

RESULTS

Physical Parameters

With the exception of April and May, temperatures were slightly cooler at Blevins Creek than at Goalders Creek (Table 2). Salinity within Goalders Creek was reasonably stable considering its meso-oligohaline location (Table 2). Except for a brief period in spring, Blevins Creek was polyhaline during the period of spot residence (salinity range 18-22‰). Salinity in Goalders Creek was always at least 4‰ lower than Blevins Creek and reached a maximum difference of 14‰ during April. Such variations in tidal creeks is typical of the estuarine salinity gradient with distance from the head of the estuary (Weinstein 1979; Weinstein et al. 1980). There were no distinct salinity differences observed between either creek and its adjacent shoal station.

Temporal Abundance and Distribution

Monthly abundance and distribution patterns for spot in each creek system and adjacent shoals are shown in Figure 2. Overall, numbers of spot captured within the tidal creeks were similar, 2,355 versus 2,802 in Goalders and Blevins Creeks, respectively. Temporal distributions of spot within each locality were further compared by computing creek/shoal ratios.

Spot were not encountered during the first sampling trip during late March 1982, but postlarvae and juveniles appeared in small numbers in April. At that time, spot were more abundant at the shoal stations than in the creeks (creek/shoal ratio of 0.28 for Goalders and 0.16 at Blevins). Young-of-year spot reached their maximum abundance in May, with 1,047 specimens taken up-estuary at Goalders Creek and 2,110 individuals sampled from Blevins Creek. Spot at Goalders Creek were then more numerous at the stations within the creek (ratio 20.5), but still more prevalent on the shoal down-estuary at Blevins Creek (ratio 0.52). From June to September, however, spot were clearly more abundant in the creeks of both systems. By the end of the investigation (October 1982) spot once again dominated the shoal at Blevins Creek, but remained more abundant in the creek at Goalders.

Monthly size distributions of spot in the two tidal creeks and adjacent shoals were examined by dividing the samples taken at each station into 5 mm SL size classes and comparing their relative frequencies among stations and locations. With the exception of a short period during recruitment (May) when more small fish were collected in Goalders Creek than at the nearby shoal station, none of the size-frequency comparisons differed significantly (Friedman's ANOVA, $P < 0.05$; O'Neil 1983).

TABLE 2.—Monthly temperature (°C), salinity (‰), and values and sediment analysis (% total dry weight) by trawl station, York River estuary, 1982.

Month	Goalders Creek			Blevins Creek		
	Upstream	Downstream	Shoal	Upstream	Downstream	Shoal
Mar.	11.0 (2.0)	11.0 (2.0)	11.0 (2.0)	9.5 (16.0)	9.5 (16.0)	
Apr.	13.5 (5.0)	13.5 (5.0)	15.0 (7.5)	16.0 (18.0)	16.0 (18.0)	17.0 (19.0)
May	20.5 (10.0)	20.0 (10.0)	21.0 (11.0)	24.0 (16.0)	24.0 (20.0)	24.0 (18.0)
June	26.0 (7.0)	26.0 (7.0)	26.0 (8.0)	25.5 (20.0)	25.0 (19.0)	25.0 (18.0)
July	29.0 (10.0)	29.0 (13.0)	29.0 (13.0)	28.0 (22.0)	28.0 (20.0)	29.0 (22.0)
Aug.	28.0 (11.0)	28.0 (11.5)	28.5 (10.0)	27.0 (22.0)	27.0 (19.5)	27.0 (20.0)
Sept.	26.0 (13.0)	26.0 (14.5)	26.0 (16.0)	25.0 (21.0)	26.0 (21.0)	25.0 (20.0)
Oct.	16.5 (11.0)	17.0 (11.0)	17.0 (12.0)	14.0 (20.0)	14.5 (22.0)	15.0 (20.0)
Sediments	(Sample cores taken in May)					
Sand and gravel	83.45	29.86	11.06	52.21	59.07	93.07
Silt	7.72	27.29	43.87	33.83	27.92	3.05
Clay	8.83	42.85	45.07	13.96	13.01	3.83
Organics	9.12	15.96	10.79	4.09	5.16	0.74

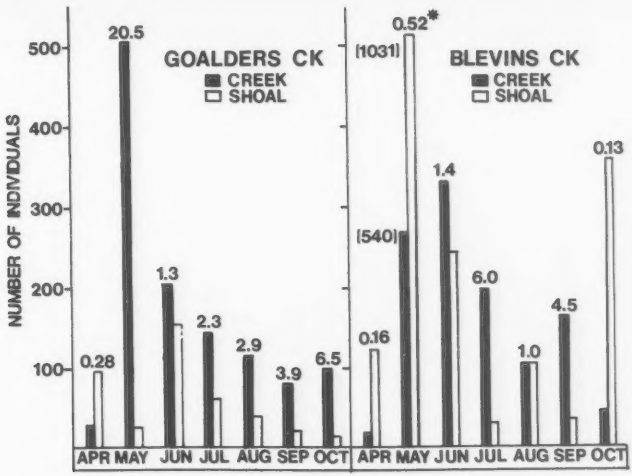

FIGURE 2.—Relative densities of spot at tidal creeks (values shown are monthly means of both creek stations) and shoal sampling localities. Asterisk indicates that May values for Blevins Creek are drawn to half scale. Values above histograms are ratios of creek to shoal densities.

Trophic Analysis

During this study, over 1,750 spot stomachs were removed and analyzed. In both creeks, spot underwent size-related, as well as temporal and spatial, changes in food utilization. Food utilization differences owing to size-related (ontogenetic) changes were examined by cluster analysis (Fig. 3). Calanoid copepods were the dominant prey of the smallest spot size classes (Fig. 4). The 26-30 mm size class had begun to consume more substrate-oriented prey (polychaetes and nematodes). All the spot examined between 40 and 100 mm SL had considerable overlap in a wide variety of food items. The great majority, however, were benthic organisms, e.g., maldanid and nereid polychaetes, *Leptocheirus* amphipods, free-living nematodes, and oligochaetes. Spot over 101 mm were clustered separately because of *Leucon americanus* in the diet. It thus appears that ontogenetic changes in spot diet shifted from a specialist mode when small to a more opportunistic strategy in larger size classes.

Size-class data were also subjected to reciprocal averaging ordination (Fig. 4). Results closely parallel those in the numerical classification. Axis 1, accounting for 49% of the variance, defined the small, planktonic size classes, which consumed mostly calanoid copepods. The spot over 101 mm were separated along Axis 2, with *Leucon americanus* and *Monoculodes edwardsi* the dominant food items. The remaining size classes lay in the plane of Axes 2 and 3 in association with a large variety of benthic prey.

The dendrogram representing the differences between stations for all size classes of spot pooled (Fig. 5) indicated that there are two main clusters that correspond to the food distinctions between the two creeks. In addition, both shoal stations clustered as distinct outliers.

Dominant prey items at the Goalders Creek sites included nereid polychaetes, clam siphons, a gammarid amphipod (*Leptocheirus plumulosus*), and harpacticoid copepods. At Blevins Creek, spot utilized proportionately more nematodes, maldanid polychaetes, and oligochaetes. At both locations spot made significant use only of specific parts of some prey items, i.e., clam siphons and tails of maldanid polychaetes (Currin et al. 1984).

Prey utilization differences were also noted between the creek stations and the adjacent shoal. At Goalders Creek the amphipod *Monoculodes edwardsi*, which dominated feeding on the shoal, was partially responsible for the separation noted in the dendrogram (Fig. 5). In the polyhaline sys-

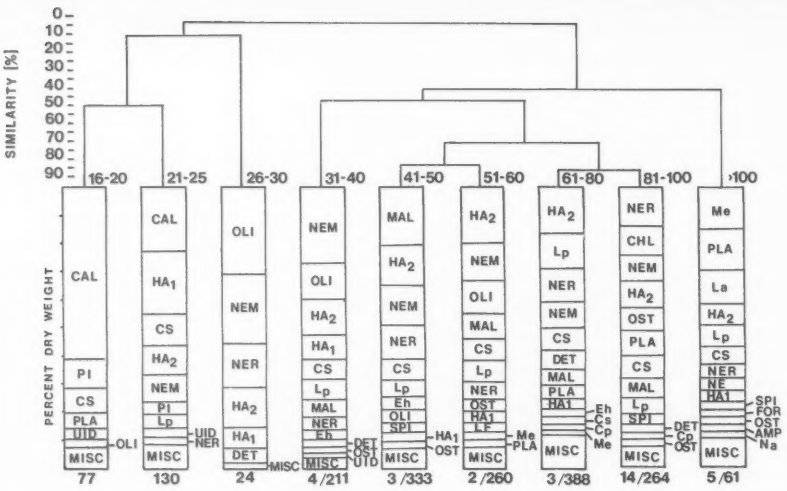

FIGURE 3.—Cluster analysis of prey similarity among *Leiostomus* size classes for the York River estuary, 1982. Prey abbreviations are listed in Table 1. Ratios at bottom of each column represent number of empty stomachs/ total sample size.

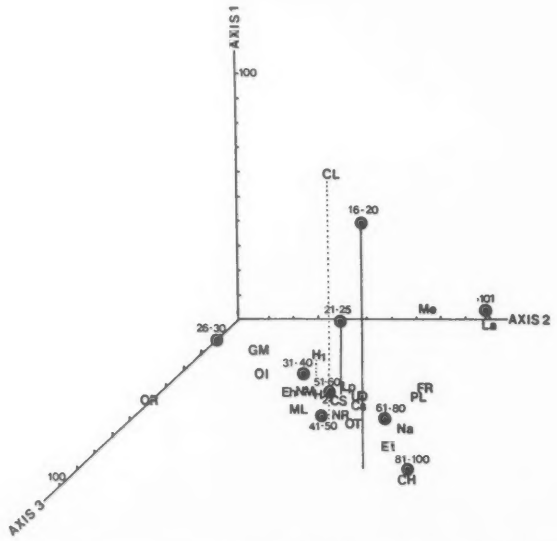

FIGURE 4.—Reciprocal averaging of prey and spot size class. Prey abbreviations: CH = Chlorophyta, CL = Calanoid copepods, Cs = *Crangon septemspinosa*, Eh = *Eteone heteropoda*, Et = *Edotea triloba*, FR = Foraminifera, GM = Gammaridae, H_1 = Small harpacticoid copepods, H_2 = Large harpacticoid copepods, La = *Leucon americanus*, Me = *Monoculodes edwardsi*, ML = Maldanidae, Na = *Neomysis americana*, OL = Oligochaeta, OR = Orbiniidae, OT = Ostracods, PL = Plant matter.

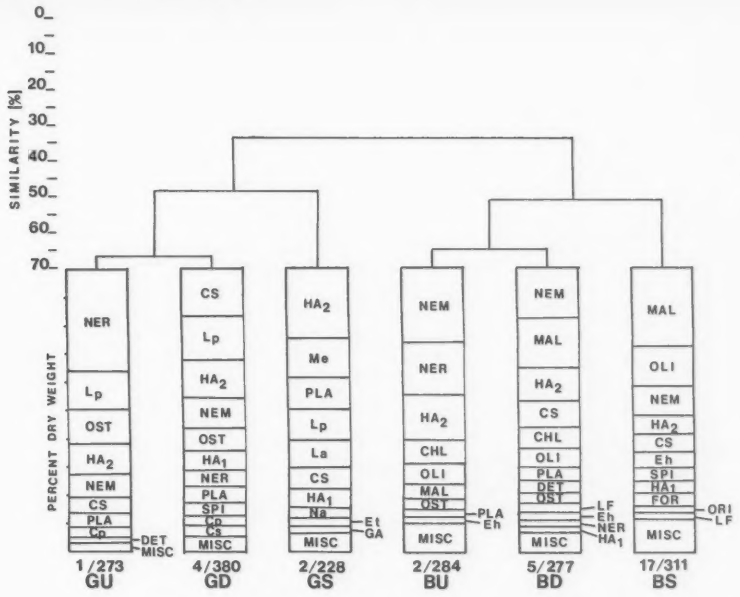

FIGURE 5.—Cluster analysis of prey similarity among habitats for spot from a polyhaline (BD = Blevins downstream, BU = creek, VA, 1982. Prey abbreviations are listed in Blevins upstream, BS = Blevins shoal) and a meso-oligohaline (GU = Goalders upstream, etc.) tidal Table 1. Ratios at the bottoms of each column represent number of empty stomachs/total sample.

tem, however, there were few clear differences caused by presence or absence of particular prey types. Instead, it was more a question of which food item was dominant. Spot appeared to eat more nematodes within the creek and more maldanid polychaetes on the shoal.

To confirm the results of the classification analysis, reciprocal averaging was used on the same food-habitat matrix (Fig. 6). Prey items located near a given station "lollipop" are the dominant food items utilized by spot at that station. Axis 1, accounting for 45% of the data variance, clearly separated the low and high salinity creek systems. Axis 2 (28% of the variance) isolated the shoal stations relative to the intracreek sites. Nematodes and maldanid polychaetes were again closely associated with the Blevins Creek sites. Nereids, *Leptocheirus*, and *Monoculodes* were dominant at the Goalders Creek habitats.

To compare seasonal patterns in food utilization between habitats, classification dendrograms were also constructed using monthly data for each creek (Figs. 7, 8). At Goalders Creek there was little overlap of prey utilized in April compared to all other months (Fig. 7). The main reason for this appears to be the large proportion of calanoid copepods consumed in April. August and October were grouped together because of the amount of nereids eaten, and the remaining months were added to this cluster individually, depending on their overall dissimilarity.

April was also an outlier at Blevins Creek, because of the dominance of calanoids in the diet of young spot (Fig. 8). May and June were clustered together because of the similarity in the consumption of maldanid polychaetes and nematodes. August and September were similar in the proportions of four prey items utilized: maldanids, nematodes, nereids, and harpacticoid copepods. Although these food items were probably incidental in their diet, July was a separate group because of the large amount of Chlorophyta present in the stomachs examined from that month; October was isolated because Foraminifera became an important addition to the diet.

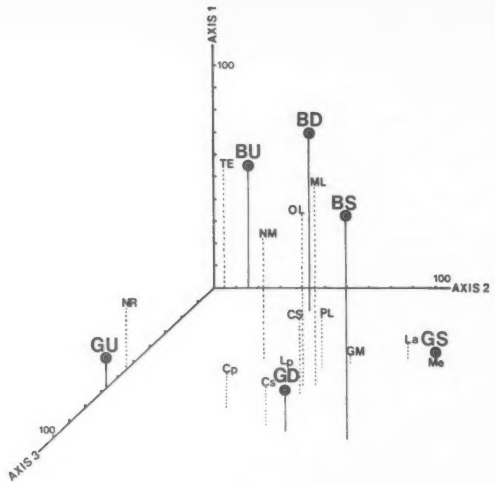

FIGURE 6.—Reciprocal averaging of prey and habitat for spot collected from tidal creeks and adjacent shoals of the York River, VA, 1982. Station abbreviations are the same as Figure 4. Prey abbreviations: Cp = *Cyathura polita*, CS = Clam Siphons, Cs = *Crangon septemspinosa*, GM = Gammaridae, Lp = *Leptocheirus plumulosus*, Me = *Monoculodes edwardsi*, ML = Maldanidae, NM = Nematoda, NR = Nereidae, OL = Oligochaeta, PL = Plant Matter, TE = Teleostei.

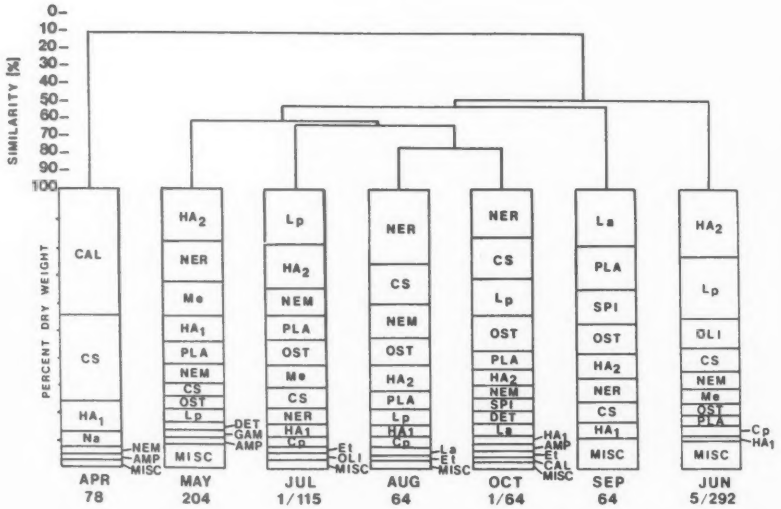

FIGURE 7.—Cluster analysis of monthly differences in prey utilization for young-of-year spot at Goalders Creek, VA, 1982. Prey abbreviations listed in Table 1. Ratios at the base of each column represent number of empty stomachs to total sample size.

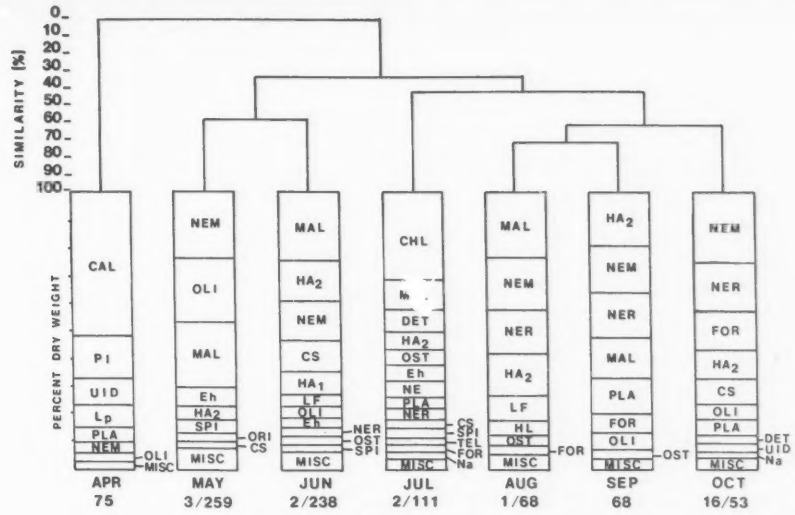

FIGURE 8.—Cluster analysis of monthly differences in prey utilization for young-of-year spot at Blevins Creek, VA, 1982. Prey abbreviations listed in Table 1. Ratios at base of each column represent number of empty stomachs/total sample.

DISCUSSION

As Livingston (1982) stated, "While food habits of fishes have been studied extensively, specific relationships of trophic interactions, habitat partitioning, and spatial/temporal variability of coastal fishes remain largely undetermined." While a more comprehensive understanding of these processes awaits properly designed experiments and hypothesis testing, several common patterns have begun to emerge. Despite the apparent abundant resources of the estuary as a whole, there seems to be a consistent "tracking" (among species) of these resources, reminiscent of resource partitioning in other aquatic systems (e.g., coral reefs). Individual species distributions are probably controlled by physiological constraints, predation pressure, and the availability of food (or a combination of these factors). That this tracking process, if real, may result from periodic scarcity of food in estuaries was tentatively stated by Thayer et al. (1974) and only recently reinforced by the studies of Weisburg and Lotrich (1986). The latter authors used experimental techniques to demonstrate food limitation occurring in the mummichog *Fundulus heteroclitus*, among fishes perhaps the most "perfectly" adapted food generalist in the estuary.

We did not observe differences in relative fullness of spot stomachs between the two creek localities examined (O'Neil and Weinstein, unpubl. data). Therefore, suitable food appears to be readily available in both creeks. The types of prey utilized in each area, however, were different and generally followed the temporal and spatial distributions of the dominant macrobenthos in these creeks (Robert Diaz[4]). Spot apparently feed opportunistically on the available resources present in the tidal creeks and shoals at any one time and do well throughout the estuary. There were no differences in growth rates or condition of spot observed in the tidal creeks in our study (Weinstein and O'Neil[5]). Thus, from an energetics standpoint, spot seem able to achieve similar growth rates in different creeks (and corresponding salinity regimes).

Hodson et al. (1981) noted that individual stomachs of small spot captured in the Cape Fear estuary were typically dominated by a single food cat-

[4]Robert Diaz, Virginia Institute of Marine Science, Gloucester Point, VA 23062, pers. commun. July 1983.

[5]Weinstein, Michael P., and Steven P. O'Neil. manuscr. in prep. Virginia Institute of Marine Science, Gloucester Point, VA 23062.

egory. This was also observed in the present investigation. Individual stomachs from spot captured in the same sample were often found to contain thousands of harpacticoid copepods or were completely distended by half a dozen nereid polychaetes. Such observations reinforce the notion of opportunism and feeding activities related to the concentration and availability of prey.

Spot, as well as other estuarine sciaenids, undergo distinct ontogenetic changes in feeding mechanisms with increasing size (Chao 1976; Chao and Musick 1977; Govoni 1981). Postlarvae and small juveniles are characterized by large eyes and a terminal mouth. They prey on mainly pelagic calanoid copepods and other small plankton (Townsend 1956; Peters and Kjelson 1975; Kjelson et al. 1975; present study). April was an outlier in the seasonal dendrograms of Figures 6 and 7 because the majority of spot at that time were in the smallest size class in Figure 8 and fed on mainly calanoid copepods. Although Thayer et al. (1974) concluded that food for meroplanktonic life stages of estuarine fishes may be limiting, we observed no differences in feeding success between spot consuming plankton and those eating benthos.

At about 20 mm SL, spot become more benthic oriented, feeding on various epifauna and infauna (Livingston 1982; present study). Sheridan (1979) also noted a distinction in prey utilization of smaller spot (20-29 mm). In the habitats of Florida's Apalachicola Bay, however, he noted that individuals in this size class consumed more insect larvae and polychaetes than copepods. His larger size classes utilized more bivalves. The difference between his observations and those in our study may simply be due to the difference in prey availability at the various locations. It should also be noted that other studies on the food habits of spot failed to recognize any size-related differences (Roelofs 1954; Darnell 1958; Stickney et al. 1975; Chao and Musick 1977; Hodson et al. 1981). This is possibly due to the selective nature of the gear used. Large seines and trawls fail to sample small fish (Chao and Musick 1977), and block netting in the high marsh may select against large fish (Hodson et al. 1981).

The dominant prey items consumed by spot in each habitat, and the basis for intercreek and shoal versus creek differences observed during our study, are partly explained by distribution patterns of macrobenthic invertebrates reported by Boesch (1977) for the York River, VA. Although that study was conducted several years before ours, and were restricted to the river shoals and channels, there is a close parallel between the patterns Boesch described and the diet of spot from similar localities within the York River. Boesch described a group of species that were "characteristically abundant in salinities of 10-20‰ throughout the Chesapeake Bay system but were not usually as abundant in higher salinities except in shallow water habitats or following disturbances." He referred to them as euryhaline opportunists that were important dietary constituents of spot at both creeks in our study.

Most of the identifiable polychaetes encountered in spot stomachs were from this group, e.g., *Nereis succinea*, *Eteone heteropoda*, and *Paraprionspio pinnata* (Spionidae). The cumacean *Leucon americanus* also belongs to this group and together with the amphipod *Monoculodes edwardsi* was consumed in large quantities by spot on Goalders shoal (Fig. 8). *Monoculodes* is a member of the group Boesch described as estuarine endemics, which are most frequent in meso-oligohaline areas. Down-estuary at Blevins Creek, the maldanid polychaetes, especially *Clymenella torquata*, figured prominently in spot diets and were determined to be most abundant in that vicinity by Boesch.

In another study, Boesch (1973) examined macrobenthic distributions as related to sediment composition and seasonality in Hampton Roads, VA. Those results give further insight to prey availability for the habitats and time periods described in the present study. Boesch (1973) found *Eteone heteropoda* more common in May and rare in August, but distributed over all sediment types in the areas of lower salinity. This species was commonly consumed by spot at Blevins Creek in May, June, and July (Fig. 7). Another polychaete, *Polydora ligni*, was common in stomachs from Blevins Creek only in April, and Boesch (1973) noted it was more abundant in the estuary between February and May. *Clymenella torquata*, also consumed at Blevins Creek, was less abundant seasonally but showed a preference for muddy-sand sites. This species was a dominant component in the diet of spot at the downstream and shoal stations, both of which had higher proportions of sand compared to the upstream station. Two polychaetes, *Nereis succinea* and *Paraprionospio pinnata* (Spionidae), were found by Boesch (1973) in sand-mud and mud-sand sediments, respectively, which generally characterized the Goalders upstream and downstream substrates, respectively (Table 2). Thus, it is likely

that spot feed on seasonally and spatially dominant prey types from the available array and that the observed differences between creeks and shoals simply reflect availability of dominant prey types. The diversity of food types in spot stomachs may also reflect the general strategy of the feeding opportunist, which is favored when 1) food densities are periodically low and there is a premium on the ability of the predator to take a range of prey, 2) the predator has a relatively long period to gain energy, and 3) prey densities fluctuate widely (Schoener 1969). These are characteristics of the marsh habitats that spot frequent as well as the general life history strategy of spot in terms of spawning season and residence period in the primary nurseries (Weinstein 1981; Weinstein and O'Neil 1986).

Finally, there is the question posed in the introduction to this paper, i.e., the relative role of these tidal creeks as feeding versus refuge zones. As suggested in the introduction and discussed above, there seeemed to be adequate food for growth of spot in tidal creeks and shoal areas, at least during the year of this study. This observation was confirmed in a separate effort using increments of daily growth observed in the otoliths of spot collected in Goalders and Blevins Creeks in 1983, and in the same two creeks plus a mesohaline creek (Kings Creek, also located in the York River system) in the following year 1984 (Weinstein and O'Neil fn. 5). Unfortunately, comparative data on the mortality of spot in different tidal creeks and other habitats are not readily available. Weinstein and Walters (1981) reported evidence of differences in spot mortality among creeks in different marshes of the Cape Fear River estuary. Mortality was significantly higher in the polyhaline marshes of the Cape Fear system in 1977, and although the mean value was highest in the same marshes in 1978, the overall variability of the data resulted in a nonsignificant difference among marshes. Mortality rates calculated for spot in the studies of Weinstein (in press) and Weinstein et al. (1984) in Little Monday Creek and Blevins Creek (located about 1 km apart) differed from the values reported for polyhaline creeks in the Cape Fear estuary 0.029 and 0.015/day versus 0.061 and 0.052/day, respectively. The difference in mortality rates calculated for the two studies lies partly in the age distribution sampled from each population (youngest age cohorts were not sampled in the York River), but this factor alone is not believed to account for all of the difference in the rates. The role of differential mortality in shaping the population dynamics of this species is clearly in need of further study.

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ASSESSMENT OF MORTALITY IN AN OFFSHORE POPULATION OF QUEEN CONCH, *STROMBUS GIGAS* L., IN SOUTHWEST PUERTO RICO

RICHARD S. APPELDOORN[1]

ABSTRACT

A Jolly-Seber multiple tag-recapture experiment was conducted for 2 years on a queen conch population offshore of La Parguera, Puerto Rico in order to estimate mortality rates. Over 2,000 individuals were tagged in 9 sampling periods spaced at 3-month intervals from August 1983 to August 1985. The occurrence of fishing in half the intervals allowed estimates to be made of both fishing and natural mortality rates. Fishing mortality averaged 1.14 over the study period. An upper limit of natural mortality including effects of emigration, was estimated to be 1.53. Assuming random diffusion, emigration was estimated and subtracted from the above yielding a corrected value of natural mortality of 1.05.

The queen conch, *Strombus gigas*, is one of the most valuable fishery resources of the Caribbean. Under heavy fishing pressure, stocks throughout the region have declined (Brownell and Stevely 1981), and the need for management has become increasingly obvious. Ideally, management decisions should be based on a firm understanding of queen conch biology, stock dynamics, and rates of exploitation. Estimates of natural and fishing mortality rates are fundamental to understanding the dynamics of exploited populations and are prerequisites of many stock assessment techniques, e.g., yield-per-recruit analysis (Beverton and Holt 1957).

All previous reports of natural mortality rate in queen conch populations have been made using only juveniles (Alcolado 1976; Baisre and Paez 1981; Wood and Olsen 1983; Berg 1976). There are two primary reasons for this: 1) populations where adult queen conch are not fished have not been studied or assessed, thus mortality estimates would include losses due to fishing as well as from natural causes; 2) estimates derived from length-frequency analysis cannot be made for adults because growth in length ceases at the onset of sexual maturity. These past estimates of natural mortality rate have all been high, ranging between 1.0 and 4.0, depending upon the age-group studied, except those of Wood and Olsen (1983) who reported values of 0.19 and 0.04 between ages 1 and 2 and ages 2 and 3, respectively. Thus, there is a dichotomy among reported values. Intuitively, it is difficult to predict whether high or low values of natural mortality rate should be expected. A low value of natural mortality rate, comparable to that of Wood and Olsen, might be expected for *S. gigas* because, in general, natural mortality is inversely related to size (Ursin 1967; Peterson and Wroblewski 1984; Blueweiss et al. 1978; Pauly 1980) and other large mollusks, from temperate areas, have typically low values of natural mortality. However, natural mortality should also be significantly related to temperature, both directly and through growth-rate mediated effects (Pauly 1979, 1980). Thus, higher values should be expected in tropical species. A casual literature review revealed only one estimate of natural mortality (M) in tropical mollusks for comparative purposes: $M = 3.66$ for the aplysiid gastropod *Dolabella auricularia* from the Philippines (Pauly and Calumpong 1984).

In the present study, rate of mortality was estimated for an offshore queen conch population spanning a wide size range and including both juveniles and adults. The Jolly-Seber multiple tag-recapture method was used. Separate estimates were made during periods of fishing and nonfishing, thus allowing partitioning of mortality into its fishing and natural components.

METHODS

The study area was located in southwest Puerto Rico, 7 km south of La Parguera (Fig. 1). The area has a uniform depth of 17 m and consists of a broad, patchy sand and macroalgal plain with oc-

[1]Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico 00709.

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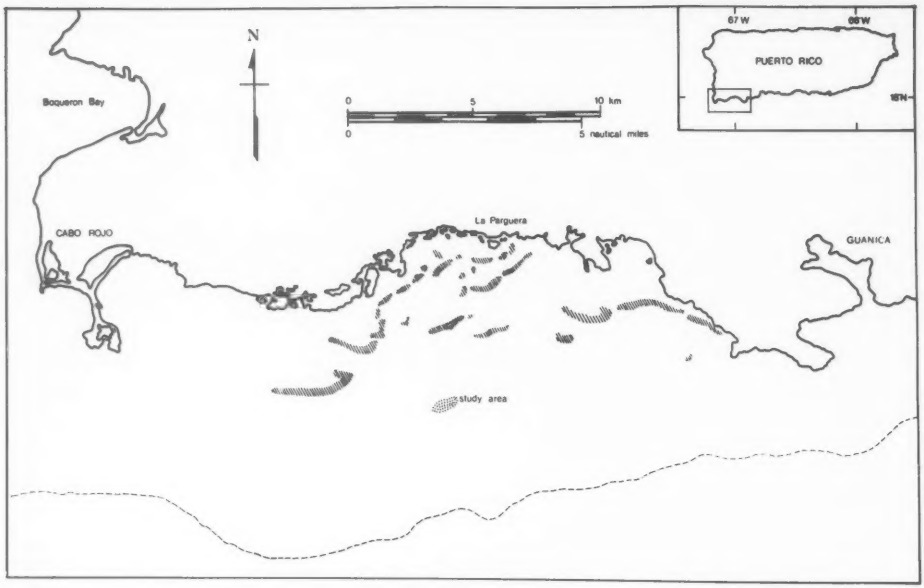

FIGURE 1.—Location of the queen conch study area (stippled) off La Parguera, Puerto Rico. Dashed line is the edge of the insular shelf. Shaded areas are emergent coral reefs.

casional patch reefs. The total study area is estimated to be 0.4 km^2, although for the first two periods sampling was limited to approximately the eastern 50% of the area.

Sampling occurred quarterly, generally in the latter half of August, November, February, and May, resulting in 9 sampling periods spanning 2 years from August 1983 to August 1985. Sampling during each period was conducted in the following manner. The area was surveyed by scuba divers and all data were collected in situ. Attempts were made to locate a minimum of 200 individuals. The maximum number was variable and subject to limits on queen conch density, the time dedicated to sampling (generally 3 weeks), and the weather during that time. During each period a two-stage haphazard sampling plan was used. Dive sites were located haphazardly throughout the full range of the study area, and the bottom covered during each dive was a function of direction and distance travelled, which also were determined haphazardly.

All queen conchs were tagged, when initially encountered, and measured for siphonal length to the nearest 1 mm using calipers. In addition, adults, defined by the presence of a flared shell-lip, were measured for lip-thickness in a similar manner. Tags consisted of 4.5 cm strips of Dymo[2] label tape, upon which a unique identification number was embossed. They were tied around the shell spire with nylon line (Fig. 2). The spines characteristic of queen conch shells held the tag firmly in place. Upon subsequent sightings tag number was recorded and shell dimensions remeasured.

During the 2-yr study period, casual assessments were made of fishing activity in the area. This was easy to do routinely as fishermen were willing to return tags from fished shells, and the presence of newly fished, empty shells on the bottom (left behind after meat extraction) was obvious after fishing had occurred. When encountered, tag numbers of these shells were recorded.

Data analysis used the Jolly-Seber method. The theory and practical mechanics of the method are presented in detail by Seber (1982: Section 5.1). It is valid for open populations where the effects of

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

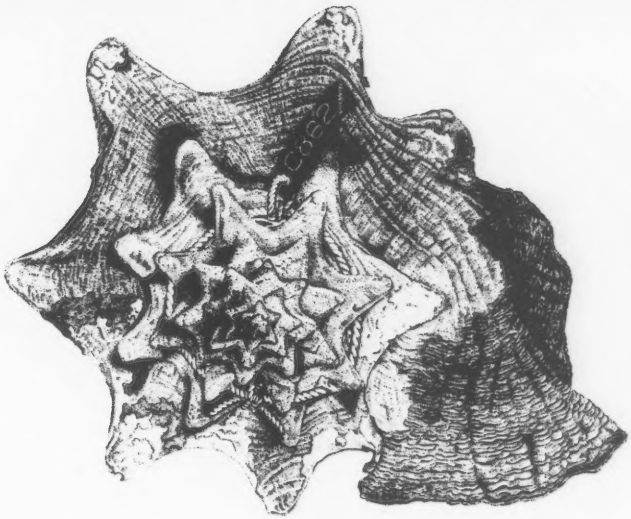

FIGURE 2.—Posterior view of adult *Strombus gigas* with numbered tag tied around the shell spire.

mortality, emigration, and recruitment can be significant between sampling periods. The assumptions of the method and their relation to the present sampling design are presented in the Discussion.

RESULTS

Over 2,000 individual queen conchs were tagged, spanning a range from 9 cm to 28 cm in length. Adult queen conchs averaged 24 cm in length and represented between 22% and 59% of sample populations, varying due to fishing activity and juvenile recruitment.

Tag return data are given in Tables 1 and 2 according to the methods in Seber (1982), with the results of the analysis given in Table 3. At any given time, roughly one-quarter of the population in the study area was tagged (Table 3, col. 2). Note the effect of increasing the sampling area at time 3 had on the estimate of abundance (N) at that time and on the estimates of survival (S) and

TABLE 1.—Tabulation of the number of queen conchs caught in the ith sample last caught in the hth sample (after Seber 1982). i and h designate sampling periods; n_i = number of conchs caught in the ith sample; R_i = number of conchs released at the ith sample; r_h = total number of conchs recaptured, last caught in the hth sample; m_i = number of conchs recaptured in the ith sample.

i	1	2	3	4	5	6	7	8	9	
n_i	424	196	275	228	352	375	262	231	227	Total
R_i	424	196	275	228	352	375	262	231	—	(r_h)
h										
1		42	28	19	22	8	1	0	0	120
2			18	7	17	6	0	0	0	48
3				10	9	2	0	2	0	23
4					40	14	5	1	1	61
5						76	22	3	2	103
6							37	13	4	54
7								35	22	57
8									36	36
m_i	0	42	46	36	88	106	65	54	65	

TABLE 2.—Tabulation of the number of queen conchs caught in the *i*th sample last caught in or before the *h*th sample (after Seber 1982). *i* and *h* designate sampling periods. z_i = number of different individuals caught before the *i*th sample which were not caught int he *i*th sample, but were caught subsequently, and is equal to the sum across the row excluding the diagonal element.

i	1	2	3	4	5	6	7	8	9	Total
h										
1		42	28	19	22	8	1	0	0	$z_2 = 78$
2			46	26	39	14	1	0	0	$z_3 = 80$
3				36	48	16	1	2	0	$z_4 = 67$
4					88	30	6	3	1	$z_5 = 40$
5						106	28	6	3	$z_6 = 37$
6							65	19	7	$z_7 = 26$
7								54	29	$z_8 = 29$
8									65	

TABLE 3.—Population estimates for queen conch derived from the Jolly-Seber multiple mark-recapture analysis. *M*/*N* = proportion of marked conchs in the population just before sample *i*; *N* = population abundance just before sample *i* with standard deviation $\hat{\sigma}[N/N]$ and coefficient of variation $\hat{\sigma}/N$; *S* = proportion surviving from the *i*th to (*i* + 1) th sample with standard deviation $\hat{\sigma}[S]$ and coefficient of variation $\hat{\sigma}/S$; *B* = number of new individuals joining the population between the *i*th and (*i* + 1) th sample with standard deviation $\hat{\sigma}[B]$ and coefficient of variation $\hat{\sigma}/B$.

i	*M*/*N*	*N*	$\hat{\sigma}[N/N]$	$\hat{\sigma}/N$	*S*	$\hat{\sigma}[S]$	$\hat{\sigma}/S$	*B*	$\hat{\sigma}[B]$	$\hat{\sigma}/B$
1	—	—	—	—	0.8387	0.1196	0.1426	—	—	—
2	0.214	1,629	310	0.1905	1.8956	0.4474	0.2360	2,585	1,017	0.393
3	0.167	5,673	1,437	0.2532	0.2372	0.0535	0.2257	409	324	0.792
4	0.158	1,754	341	0.1946	0.4706	0.0626	0.1330	62	148	2.398
5	0.250	888	106	0.1191	0.7359	0.1096	0.1490	608	136	0.223
6	0.283	1,261	196	0.1557	0.2913	0.0493	0.1692	361	89	0.246
7	0.248	729	117	0.1602	0.6208	0.1202	0.1937	542	152	0.280
8	0.234	995	205	0.2059	—	—	—	—	—	—
9	0.286	—	—	—	—	—	—	—	—	—

recruitment (B) between times 2 and 3. These figures are obviously unrealistic (e.g., survival cannot be greater than one) and are not considered in any subsequent analysis or discussion.

Survival rates of queen conch varied from 0.839 to 0.237 with coefficients of variation varying from 13.3% to 22.5%. Intensive fishing was known to have occurred in the study area between samples 3 and 4, and 6 and 7. Fishing also occurred between samples 7 and 8, but to a much lesser degree. In the former two periods estimated survival rates were the lowest found: 0.237 and 0.293, respectively. Survival estimates from all other periods represent the effects of only natural mortality and emigration. The average of these 3 values is 0.6817. This would correspond to an instantaneous rate of natural mortality per 3-mo period of 0.3832 [$= -\ln(1 - S)$] if no emigration occurred. Assuming the effects of emigration are constant between sampling periods, estimates of instantaneous fishing mortality can be obtained by subtracting the average value of instantaneous natural mortality (which includes any emigration effect) from instantaneous total mortality for periods of known fishing activity. For sampling periods 3-4, 6-7, and 7-8, the instantaneous rates of fishing mortality per 3-mo period were, respectively, 1.056, 0.845, and 0.0935. Dividing the sum of these by the total time period for which mortality estimates are available (1.75 year) results in an estimate of the annual instantaneous fishing mortality rate (F) for the population in the study area of 1.14 between August 1983 and May 1985.

On an annual basis, the apparent instantaneous rate of natural mortality for queen conch is 1.533. However, this overestimates true natural mortality because permanent emigration was known to occur, and it was not possible to precisely quantify the effects of emigration on the basis of these data (see Discussion). The estimate does provide an upper bound on the value of natural mortality.

DISCUSSION

Model Assumptions

Principal assumptions of the Jolly-Seber method are that sampling is random, with catch-

ability equal for all individuals, that rates of survival are equal for all individuals, and that tag loss is negligible. No field study can hope to manipulate the environment to such a degree that all assumptions are perfectly met. Thus, potential deviations from these assumptions must be considered and their significance and resulting implications assessed (Begon 1983). Presented below is a review of each assumption. Based on known or suspected aspects of the biology and ecology of queen conch, potential problems with respect to each assumption are raised. Each potential problem is then considered in light of the specifics of the present study, and an attempt is made to assess its significance, if any. Finally, consideration is given to the robustness of Jolly-Seber estimates. In general, it will be shown that deviations from Jolly-Seber assumptions, if present, would be small and have little impact, and in addition, the Jolly-Seber method is robust to such deviations.

In the present study, sampling was conducted on an areal basis. Although sampling was not truly random (i.e., with areas predetermined in a random fashion), dive sites were spread throughout the study area and chosen without prior reference to, or knowledge of, the specific nature of the habitat or conch density in the immediate area. The two stage sampling design employed allowed every section of the study area to have an equal probability of being covered. The assumption of equal catchability is the more important property here, and there were several points where potential departures from this assumption could have arisen. Queen conchs usually showed a distinct clustered distribution. Within a cluster all individuals were felt to have an equal probability of capture, regardless of size. However, large queen conchs were easier to see at a distance. This would affect capture probabilities if distinct size groups characterized clusters; thus, clusters of large queen conchs would be noticed more frequently. While it was thought that there existed areas differentially characterized by the abundance of juveniles and adults, these areas generally occurred on a larger scale than typically covered on a dive. The random allocation of dive sites, then, should have minimized any effect of this heterogeneity. The tendency of very small queen conchs to remain buried is a second factor potentially affecting catchability. Thus, a small tagged queen conch (<13 cm) might have a reduced probability of recapture until it grows large enough to be exposed most of the time. However, only a very small fraction of queen conchs sampled would have been affected by this. By the time the animals are large enough to be sampled in significant numbers, they will, by the time of next sampling, have grown to a size where burial is not a problem; thus recapture would not be affected. In sum, for the size range sampled, it is thought that departures from the assumption of equal catchability are small, if present. Pollock and Mann (1983) and Carothers (1973) have both found Jolly-Seber estimates of survival to be robust against heterogeneity of capture probabilities.

Mortality of queen conch could have been dependent upon mark status if tags attracted predators. There is no direct evidence (e.g., observations or signs of predators or predation during tagging periods) to indicate that this problem occurred, implying that it did not. Tags quickly fouled with macroalgae and were subsequently impossible for divers to see at any distance. Thus, any tag attraction effect could only occur immediately after initial tagging. As such, the problem is thought to be negligible. Departures from equal probability of survival may have occurred owing to size related processes, but not to a serious degree. Natural mortality is thought to decrease with age, with the effect being predominant among small juveniles (Appeldoorn in press a, b). However, the majority of queen conchs sampled here were large juveniles and adults, which should have had similar survival probabilities. Although fishermen usually take all sizes of queen conchs found, large conchs should have suffered a greater mortality because generally fishermen will not dive in an area unless conchs are visible (i.e., large) from the surface or on shallow test dives. Thus, areas predominantly characterized by small queen conchs should have been undersampled by fishermen. Again, the potential effect of this is offset because the majority of conchs were large. Also, only a portion of the small queen conchs were from areas particularly characterized by such individuals. Lastly, rate of dispersion is also a function of size (Hesse 1979; Appeldoorn and Ballantine 1983), so the emigration component of survival could have been higher for larger individuals. This, to some degree, would counter the size-mortality trend, with the effect being predominant among small juveniles. As such, the effect here should also have been minor. In sum, there is no reason to suspect substantial departures from the assumption of equal probability of survival, and if survival is independent of mark status and probability of

capture is independent of age, Jolly-Seber survival estimates are not greatly affected by age-dependent mortality (Seber 1982).

There are methods available for determining age-dependent mortality rates from Jolly-Seber data (Pollock 1981; Pollock and Mann 1983). Queen conchs, however, are difficult to age (Appeldoorn 1987). Length groups could be used, but these would have to be defined narrowly so that all individuals could grow into the next largest size group within the 3 months between sampling periods, thereby reducing sample sizes within length groups to impractical levels. Data pooled over time would have forced confounding of natural and fishing mortality effects, which was deemed undesirable.

Tags were held securely in place because spines on the queen conch shell spire prevented tie lines from slipping off, and they became more secure over time due to fouling. Numbers remained readable throughout the 2-yr period. In only those individuals with poor spine development could the tag be lost, and then only within the short time prior to fouling. These included some very small juveniles (<12 cm) and a few very old queen conchs where spines had been eroded. The total number of such potential cases was exceedingly small and is, therefore considered negligible.

Estimation of Emigration and Natural Mortality

Permanent emigration of queen conch was known to occur. Reports from fishermen placed some individuals as much as 9 km away from the study area, although the time this took is unknown. The degree of emigration needs to be accounted for if a more accurate estimate of natural mortality is to be obtained. Emigration can occur by either of two dispersion processes: random diffusion, and directed migration or drift. Seasonal migrations are expected in late fall and early spring based on other studies (Hesse 1979; Appeldoorn 1985), although the expected distance travelled is unknown. However, no evidence of such migration is apparent in the data for either mortality or recruitment. Possible reasons for this are 1) the mortality component is confounded by fishing effects thereby masking seasonal trends, 2) Jolly-Seber estimates of B are typically imprecise (Seber 1982), and 3) sampling periods were too few and inopportunely placed. Since the data do not support the occurrence of significant drift, at least to the point where it can be partitioned from diffusion, the degree of emigration was estimated by analyzing diffusion only.

Skellam (1951) presented a two-dimensional diffusion model which can predict the proportion of a population (P_t) outside the area of radius (ρ_t) in a given time (t) if the average distance travelled (ϵ) per unit time (Δt) is known. Assuming no mortality or birth, the equation is

$$P_t = \exp[-(\rho_t{}^2)/(t \cdot \epsilon^2/\Delta t)]$$

To estimate emigration an average value of ϵ is needed. Dispersal ability in *Strombus* is related to size (Hesse 1979; Miller 1972; Appeldoorn and Ballantine 1983). Specifically, if total movement is expressed solely as diffusion, the data of Hesse (1979) from a 1.5-mo period encompassing episodes of both diffusion and drift indicated that adults travelled twice as fast as "maturing" queen conchs (adults with thin lips or very large juveniles) and three times as fast as juveniles. Hesse (1979) recorded adults to move commonly 50-100 m/day, but no average figure was given, and it is assumed that rates less than this were also common. Clifton et al. (1970) tracked one group of adult queen conchs at 45-55 m/day over several days. Given these rates, a value of 50 m/day seems a reasonable estimate of ϵ for adults, averaging higher values during migration with lower values at other times. The La Parguera population consists of both juveniles and adults, so this value needs to be adjusted downward accordingly. Since the majority of queen conchs were old juveniles or young adults, an average stage of "maturing" can be assumeed, and a value of ϵ, one half that for adults, would be most appropriate, i.e., $\epsilon = 25$ m/day. If it is assumed that the 0.4 km^2 study area is a circle of radius ca. 350 m, then in one sampling period (90 days) 11.2% of the population would be expected to emigrate. This results in an instantaneous rate of annual emigration equal to 0.481. Subtracting this from the estimate of natural mortality plus emigration (1.533) yields a corrected estimate of natural mortality rate at 1.05.

This value of natural mortality rate is lower, but consistent with values reported by Alcolado (1976), Berg (1976), and Baisre and Paez (1981), which might be expected since their estimates were limited to juveniles. However, it is still much greater than those reported by Wood and Olsen (1983). Hoenig (1983) presented empirical equations predicting mortality rate on the basis of oldest known age, which can be used for com-

parative purposes. Given a maximum life span of 7 years (Wefer and Killingley 1980) the predicted mortality rate is 0.72, a result compatible with the above estimate of natural mortality rate considering the variability associated with each estimate.

Status of the Fishery

The value of fishing mortality (F) relative to natural mortality (M) indicates that the La Parguera *S. gigas* population is intensely exploited. Gulland's (1971) calculation of $F = M$ at the point of maximum sustainable yield (MSY) would indicate, allowing for variability in the estimates, that the population was being fished at or above F_{MSY} at this time. However, Francis (1974) has shown that this relationship does not always hold, and Caddy and Csirke (1983) stated that tropical species in particular, already characterized by high levels of natural mortality, would be more likely to be overfished according to this formula. Using this conservative approach, a diagnosis of overfishing seems warranted. Since the study area is representative of that portion of the offshore La Parguera shelf supporting queen conch fishing, in terms of habitat, conch density, and general fishing activity, these results should have general relevance.

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POPULATIONS OF HORSESHOE CRABS, *LIMULUS POLYPHEMUS*, ON THE NORTHWESTERN ATLANTIC CONTINENTAL SHELF

MARK L. BOTTON[1] AND JOHN W. ROPES[2]

ABSTRACT

This report analyzes the distribution and abundance of horseshoe crabs, *Limulus polyphemus* (L.), on the Middle Atlantic continental shelf, based on Northeast Fisheries Center (NEFC) bottom trawl and ocean clam surveys of the past two decades at depths beginning at 9 m. Crabs were collected from North Carolina to southern New England, with the highest abundance and frequency of occurrence between Virginia and New Jersey. Approximately 90% of the minimum estimated standing stock size in that area, 2.3-4.5 million individuals, was located at depths <30 m. The geographic distribution may reflect proximity of this shelf region to the principal spawning areas in Delaware and Chesapeake Bays. Seasonally, horseshoe crab abundance on the shelf declined during those months when spawning in estuaries peaked. Crabs were caught at depths to 290 m, the limit of sampling; most of the animals caught at depths >100 m were off Cape Hatteras, North Carolina. Despite the presence of horseshoe crabs in estuaries as far north as Maine, New York is the northward limit on the shelf. This suggests that inshore populations in New England may be relatively isolated from each other and from the large Middle Atlantic shelf population.

Generalizations about the natural history, behavior, and ecological importance of horseshoe crabs, *Limulus polyphemus* (L.), are primarily based on studies of the shallow-water phase of its life cycle (Shuster 1979, 1982; Wells et al. 1983). The populations in the mid-Atlantic region are most accessible in late spring and early summer, when adults spawn en masse on sandy estuarine beaches. Knowledge of behavior (Shuster 1950; Rudloe 1980; Barlow et al. 1982; Cohen and Brockmann 1983), orientation (Rudloe and Herrnkind 1976; Botton and Loveland in press), morphometrics (Shuster 1955; Riska 1981), sediment disturbance (Woodin 1978, 1981), and predation (Smith and Chin 1951; Smith et al. 1955; Botton 1984a, b) is all based on studies of shallow-water or intertidal individuals. Population estimates have been restricted to shallow-water adults (Baptist et al. 1957; Sokoloff 1978; Rudloe 1980; Shuster and Botton 1985), with the exception of Botton and Haskin (1984), who surveyed the population on the inshore New Jersey continental shelf.

Perhaps because of the spectacular intertidal mass spawning phenomenon and accessibility, estuarine populations have received a disproportionate amount of attention by ecologists. In contrast, most of the animal's life is spent sublittorally. An adult female may spawn completely over several successive high tides; in general, repeated breeding is more characteristic of males (Rudloe 1980). Juveniles, during their first and second summer, are abundant on intertidal flats (Shuster 1955, 1979), but the remainder of the species' 14-19 year life span (Ropes 1961) is spent subtidally except for the annual spawning migration.

This report summarizes latitudinal and bathymetric distributions of horseshoe crabs on the northwestern Atlantic continental shelf. Northeast Fisheries Center (NEFC) bottom trawl and ocean clam surveys during the past two decades have provided extensive data on the abundance and distribution of horseshoe crabs, principally north of Cape Hatteras, NC (Ropes et al. 1982; NEFC unpubl. data). Seasonal and annual trends in abundance are also discussed in the present report. Concern for evaluating the general population characteristics of horseshoe crabs parallels expanding commercial exploitation of the species. Animals are presently harvested to extract blood for the *Limulus* amoebocyte lysate (LAL) test, and as bait in eel (*Anguilla rostrata*), conch (*Busycon* sp.), and other fisheries (Pearson and Weary 1980); the vast majority of the fishing ef-

[1]Division of Science and Mathematics, Fordham University, College at Lincoln Center, 113 West 60th Street, New York, NY 10023.

[2]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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fort is concentrated between Virginia and New Jersey (Botton and Ropes in press).

MATERIALS AND METHODS

NEFC bottom trawl surveys ranged from Cape Fear, NC, north to the Scotian Shelf; clam surveys cover the Middle Atlantic region north to Georges Bank. Both are general purpose survey programs, collecting data for standing stock assessments for many finfish and shellfish species, as well as collecting specimens for age determination, dietary analysis, and many other purposes (Grosslein 1969; Clark 1979).

During the period covered by this study (1975-83), the #36 and #41 Yankee otter trawls were used as sampling gear during bottom trawl surveys. Both nets have a mesh size of 5 inches throughout the wings and body, and 4.5 inches in the cod end. A liner of 0.5-in nylon mesh is employed at the aft end of the top belly and the cod end. Trawls are equipped with roller gear to facilitate use over rough bottoms. All tows were 30 minutes in duration at a vessel speed of 3.5 knots; stations were located using loran. An average of 1,129 stations per year was sampled (range, 711 stations in 1975 to 1,547 stations in 1979). Cruises were conducted during fall (September through early December) and spring (March through May) in all years, with five additional surveys during the summers (July through August) of 1977-81 and two during the winters (January through February) of 1978 and 1983. Sampling was conducted both day and night. After sorting the catch, personnel recorded the number of horseshoe crabs taken in each tow and their total wet weight to the nearest 0.1 kg.

A stratified random sampling design was used in the surveys (Grosslein 1969). The region was divided into several strata based primarily on depth. Stations were allocated to strata roughly in proportion to the area of each stratum and assigned to specific locations within strata at random (Clark 1979). For the purpose of this paper, stations of 9-27 m (5-15 fm) depth were defined as "inshore" and those deeper than 27 m as "offshore". Preliminary inspection of the catch data compiled by Ropes et al. (1982) showed the bulk of the horseshoe crab population to be located between northern New Jersey and southern Virginia. Within this region, there were 27 inshore and 16 offshore strata, based on depth and location. Stratified mean number per tow and biomass per tow of horseshoe crabs were converted into estimates of standing stock by using the "area swept" by a standard survey trawl in relation to catch as an estimate of minimum absolute density. Tows within strata were used to calculate variances around the means. Total populations for the inshore and offshore regions were estimated by expanding the average stratified mean catch per tow by the ratio of total area surveyed to the area sampled by an average tow. Further details of statistical methods are found in Clark (1979).

Ocean clam surveys used commercial style hydraulic dredges, towed for 5 minutes at 1.5 knots. The design and performance of this sampling gear is discussed by Meyer et al. (1981). Cruises from 1965 to 1978 used either a 30-in (91 cm) or 48-in (122 cm) knife-width dredge; cruises from 1979 to 1983 used a 60-in (152 cm) dredge. There were no ocean clam surveys in 1968, 1971-73, and 1975. Station locations were selected using a stratified random sampling design; the average number of stations sampled per year was 370 (range, 139 in

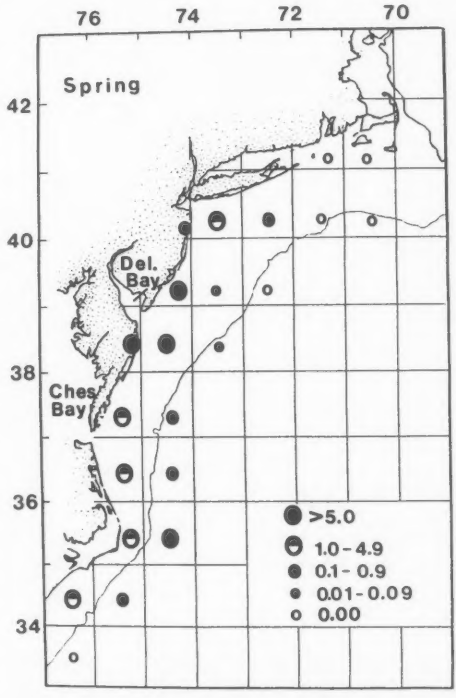

FIGURE 1.—Mean number of horseshoe crabs per tow,

1979 to 655 in 1966). Catches were not expanded into stock estimates, as for the bottom trawl survey data.

To analyze broad latitudinal variations in abundance and frequency of occurrence, catch and sampling effort were grouped by 1-degree latitude and longitude blocks. For example, stations at lat. 38°06′N, long. 74°02′W and 38°45′N, 74°50′W were both grouped together as 38°N, 74°W. Bottom trawl and ocean clam survey data were analyzed separately, because stratification schemes differed and the efficiencies of the two types of sampling gear cannot readily be compared.

RESULTS

Latitudinal Distribution

During groundfish surveys, 7,035 crabs were taken at 983 stations distributed from 33°N to 41°N; 75% of the crabs were caught between 37°N and 40°N (Fig. 1, App. Table 1). Highest abundance and frequency of occurrence was found on the sheif nearest the mouth of Delaware Bay. The maximum number of individuals per tow, 99, was obtained on 22 March 1976, from a station located off Assateague Island, VA, at 38°00′N, 75°14′W, in 13 m of water. Mean number per tow generally decreased with increasing distance from shore (Fig. 1).

Horseshoe crab abundance decreased both north of 40°N and south of 37°N (Fig. 1). Crabs were absent northeast of Montauk Point, Long Island (41°N, 72°W), and no crabs were found on or north of Georges Bank despite intensive sampling effort. Fewer than 2% of all horseshoe crabs collected were found south of 35°N (Cape Hatteras), and only one animal was caught south of 34°N.

The observed latitudinal distribution of horseshoe crabs in ocean clam surveys paralleled the above trends. A total of 1,640 animals was taken at 535 stations clustered primarily between Vir-

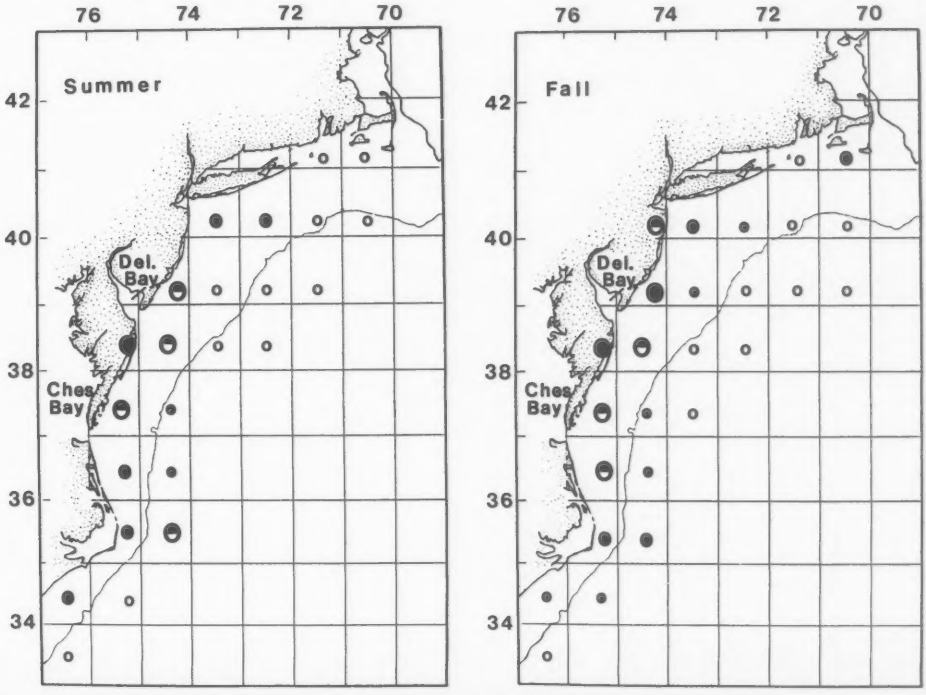

FIGURE 1.—*Continued*—by 1° latitude and longitude blocks, based on NEFC groundfish trawl data from 1975 to 1983.

TABLE 1.—Distribution of horseshoe crabs in clam surveys, 1965-83; 1,640 animals enumerated at 535 stations. Number of crabs over (number of stations with one or more individuals) in each row.

Latitude (N)	Longitude (W)			
	75°	74°	73°	72°
40°		4 (3)	23 (14)	4 (4)
39°		115 (46)	3 (3)	
38°	237 (77)	351 (103)		
37°	671 (176)	30 (16)		
36°	153 (76)	1 (1)		
35°	48 (16)			

ginia and New Jersey (Table 1). Thus, horseshoe crabs were most abundant along the continental shelf from Virginia to southern New Jersey in both groundfish and ocean clam surveys.

Seasonal and Annual Variations in Standing Stock

On the New Jersey-Virginia continental shelf, average abundance and biomass were highest during spring and fall cruises, lower in summer, and lower still (based on limited sampling) in winter (Fig. 1, Table 2). Horseshoe crabs were present in more than half the inshore tows throughout the year. Frequency of occurrence did not fluctuate as widely as abundance or biomass, and was consistently higher inshore than offshore.

Population estimates show considerable annual variation, with highest recorded catches in spring of 1976 and 1981 (Fig. 2). However, no clear trends in standing stock between 1975 and 1983 were evident. We estimate, based on the more complete fall and spring surveys, a minimum inshore population ranging from 1.8 to 3.1 million individuals (2,969 to 3,626 t), and a minimum offshore population ranging from 0.5 to 1.4 million individuals (972 to 1,975 t) (Table 2), for a total of some 2.3-4.5 million individuals. Coefficients of variation, based on individual stratum catches, ranged from 11.6 to 41.6 for individual inshore survey estimates, and from 23.6 to 87.5 for offshore estimates.

TABLE 2.—Average of seasonal variation in horseshoe crab abundance and biomass on the continental shelf, northern New Jersey to southern Virginia, based on groundfish surveys from 1975 to 1983. Strata shallower than 27 m were defined as inshore, and strata deeper than 27 m were defined as offshore.

	Winter	Spring	Summer	Fall
Inshore				
Mean no. per trawl	0.41	7.44	3.26	4.54
% occurrence	56	76	61	78
Population ($\times 10^6$)	0.410	3.103	1.258	1.881
Biomass (metric tons)	93	3,626	2,075	2,969
Offshore				
Mean no. per trawl	—	1.03	0.10	0.42
% occurrence	—	29	30	22
Population ($\times 10^6$)	—	1.445	0.129	0.530
Biomass (metric tons)	—	1,975	231	972

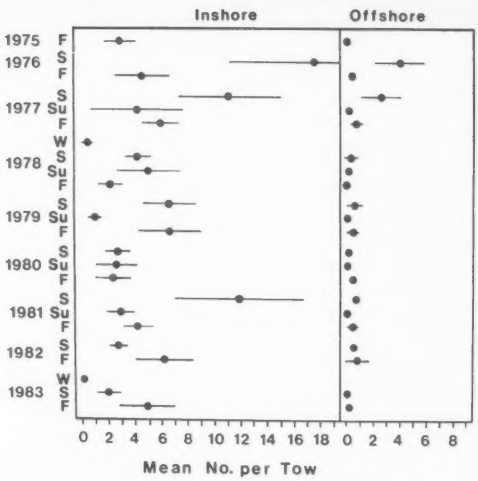

FIGURE 2.—Mean number of horseshoe crabs per tow (with 95% confidence limits) on the continental shelf from New Jersey to Virginia, based on NEFC groundfish trawl data from 1975 to 1983. W = winter; S = spring; Su = summer; F = fall; Inshore = all tows within sampling strata shallower than 27 m; Offshore = all tows within sampling strata deeper than 27 m. Where no confidence limit is shown, calculated limit was smaller than the width of the datum point.

Bathymetric Distribution

Horseshoe crabs were taken at stations between the inshore sampling limit, 9 m, and 290 m depth (Fig. 3). Seventy-four percent of the total number caught in bottom trawl surveys were taken from stations shallower than 20 m; and 92% were caught at depths <30 m. This trend was not an artifact of sampling effort. Offshore stations (>27 m) comprised approximately 73% of the sampling effort but produced <10% of the

catch. Mean abundance and biomass were nearly an order of magnitude higher at the inshore strata than the offshore strata, and horseshoe crabs were at least twice as likely to be caught inshore than offshore during all seasons (Table 2). The operation of the hydraulic clam dredge was limited to waters <80 m, and within this range, crabs were again most abundant at shallower depths. Sixty-two percent of the total catch was found shallower than 20 m, and 90% was found shallower than 30 m (Fig. 3).

Ninety-six animals were caught in 19 tows from 100 to 199 m depth, while 53 animals were taken in 7 tows below 200 m (Table 3). These deep-water individuals were caught between 34°21′N and 37°42′N (North Carolina to southern Virginia), with the majority from Cape Hatteras, south.

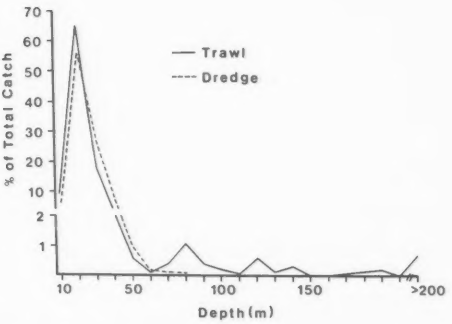

FIGURE 3.—Bathymetric distribution of horseshoe crabs, as percent of total catch, based on bottom trawl data (solid line) and ocean clam dredge data (dashed line).

DISCUSSION

Horseshoe crabs on the northwestern Atlantic continental shelf were most abundant between Virginia and New Jersey. On this section of the shelf, the population was estimated to be some 2.3-4.5 million individuals and was relatively constant between 1975 and 1983. The estimate of inshore abundance was necessarily conservative, because large survey vessels could not operate in shallow water. Horseshoe crabs may be abundant in areas inshore of the NEFC surveys; for example, in New Jersey State surveys, stations <1.8 km from shore frequently have over 10 horseshoe crabs/5-min hydraulic dredge tow in the Cape May area (Botton and Haskin 1984), and in areas of Narragansett Bay, 20-min otter trawls conducted by the State of Rhode Island have caught up to 40 horseshoe crabs (R. Sisson[3]). Both inshore and offshore stock estimates may also be conservative because the trawls, which are equipped with roller gear, may be <100% efficient in sampling horseshoe crabs, particularly if the animals are burrowed.

Seasonal surveys of the middle Atlantic continental shelf indicate a decline in horseshoe crab abundance during summer (July-August), which is consistent with the hypothesis that the shelf animals have seasonal inshore spawning migrations (Shuster and Botton 1985). More animals were caught during spring (April-early May) and fall (September-early December) periods, representing the prespawning and postspawning seasons, respectively. Therefore, the Virginia to New Jersey shelf population probably consist largely of individuals which spawn during the spring and early summer in the Chesapeake and Delaware Bays, and disperse offshore.

The range of horseshoe crabs on the continental

[3]R. Sisson, Division of Fish and Wildlife, Rhode Island Department of Environmental Management, Wakefield, RI 02879, pers. commun. December 1983.

TABLE 3.—Occurrence of all horseshoe crabs below 100 m depth on the continental shelf in groundfish surveys from 1975 to 1983.

Depth (m)	Latitude (N)	Longitude (W)	Date	Number of crabs
102	34°25′	75°53′	3/79	1
113	35°29′	74°50′	3/82	25
117	35°48′	74°52′	9/81	4
118	35°46′	74°51′	3/77	3
118	36°27′	74°47′	9/77	2
120	36°20′	74°48′	3/77	7
120	36°20′	74°48′	3/78	1
120	37°42′	74°15′	9/79	1
120	36°10′	74°48′	9/80	2
125	36°20′	74°55′	3/79	4
133	34°56′	75°21′	3/79	2
135	35°00′	75°16′	9/79	4
137	35°33′	74°49′	3/76	21
170	36°10′	74°47′	3/76	1
173	35°51′	74°52′	3/82	4
183	35°41′	74°49′	9/77	8
186	34°21′	75°55′	3/82	1
188	34°52′	74°24′	3/79	1
189	35°40′	74°48′	3/79	7
[1]189	35°39′	74°48′	9/81	7
205	35°53′	74°50′	3/76	18
205	35°37′	74°49′	10/76	12
220	35°50′	74°51′	9/79	2
228	34°27′	75°44′	9/79	1
246	36°25′	74°46′	3/76	10
290	35°20′	74°54′	3/80	3

shelf is more limited than its estuarine distribution. Although substantial shelf populations are restricted to the south and west of Long Island, NY, breeding populations are found in estuaries as far north as Hog Bay, ME (44°35′N) (Born 1977). Populations in Narragansett Bay, Barnstable Harbor, Buzzards Bay, Cape Cod Bay, and Nantucket Harbor are large enough to be commercially exploited for *Limulus* lysate and/or bait (Botton and Ropes in press). Why such populations remain close to shore is unclear. However, it is consistent with the data of Baptist et al. (1957). They showed that individuals in Plum Island Sound, MA, remained in the local area 3 years after tagging.

The more northerly horseshoe crabs may be more discrete and isolated estuarine populations than those from North Carolina to New York. The small number of crabs on the southern New England shelf suggests that migrations of crabs between estuaries may be limited, although such populations may be occurring at depths too shallow to be sampled by large vessels. However, in the September 1985 trawl survey of the territorial waters of Massachusetts, only 34 horseshoe crabs were caught at 16 of the 94 stations sampled (mean depth 28 m, range 6-76 m) with similar numbers recorded during other recent surveys (B. Kelly[4]). If, in fact, these New England populations are isolated from the large Virginia-New Jersey stock, overexploitation may have serious detrimental effects. Although horseshoe crab larvae are weak swimmers, they are not commonly found in the plankton. Dispersal between discontinuous New England estuaries therefore depends on migration of juveniles or adults. However, the issue of stock identity may require further study. Shuster (1979) argued, based on morphometric data, that horseshoe crabs formed discrete populations throughout the geographic range. On the other hand, Saunders et al. (1986) found no evidence for genetic divergence between New England and middle Atlantic populations, based on their analysis of mitochondrial DNA.

The most noteworthy feature of the bathymetric distribution was the presence of horseshoe crabs at the edge of the continental shelf, at depths to 290 m. These animals were concentrated off North Carolina, where the continental slope is much closer to shore than at any other location in the Middle Atlantic Bight. This suggests that distance from shore, rather than depth per se, limits the dispersal of crabs on the continental shelf. Horseshoe crabs are eurythermal, tolerating temperatures from −1.1° to over 40°C (Mayer 1914; Fraenkel 1960); neither of these extremes are likely on the northwestern Atlantic continental shelf. Laboratory animals in an electronic shuttlebox arrangement voluntarily occupied temperatures from 15° to 40°C (Reynolds and Casterlin 1979), but the avoidance of cooler water may not apply to all populations, as all experimental animals were indigenous to the Gulf of Mexico. Our depth record at 290 m exceeds the 200 m record of Wolff (1977) but is not the maximum depth attained by this species. A submersible camera operated by the Duke Univeristy Marine Laboratory photographed a horseshoe crab at 1,097 m depth at 32°38′N, 76°33′W (D. Bunting[5]).

The potential orientation cues directing such deep-water animals to and from estuarine spawning beaches are of interest. Rudloe and Herrnkind (1976) showed that wave surge was important in determining the orientation of crabs in shallow waters near breeding sites, while Barlow et al. (1982) found that visual cues are important in the selection of cement "female models" by spawning males. Horseshoe crab eyes are sensitive to polarized light (Waterman 1950) and to low levels of visible light, and there are a variety of endogenous morphological changes that may permit photoreceptors to have high light sensitivity (Barlow et al. 1980). Whether such physiological properties are ecologically significant in enabling crabs to orient from the edge of the continental shelf to the estuarine spawning beaches is not yet known.

Much remains to be learned about the ecological relationships between horseshoe crabs and other shelf fauna. Botton and Haskin (1984) found that adult horseshoe crabs were dietary generalists off the New Jersey coast, both in terms of taxa and sizes of food items selected. Predation by horseshoe crabs in Delaware Bay affects bivalve abundance, size-frequency patterns, and spatial distributions (Botton 1984b, c). Significant commercial fisheries for surf clams, *Spisula solidissima*, and ocean quahaugs, *Arctica islandica*, overlap the range of horseshoe crabs on the northwestern Atlantic continental shelf. A study of horseshoe crab stomach contents is in

[4]B. Kelly, Massachusetts Department of Marine Fisheries, East Sandwich, MA 02537, pers. commun. October 1985.

[5]D. Bunting, Duke University Marine Laboratory, Beaufort, NC 28516, pers. commun. April 1985.

progress which will evaluate the importance of horseshoe crab predation to these bivalves.

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APPENDIX TABLE 1.—Abundance and frequency of occurrence of horseshoe crabs on the middle Atlantic continental shelf. Based on National Marine Fisheries Service trawl surveys from all seasons, 1975 to 1983.

Latitude/ longitude	No. stations sampled	No. stations with crabs	No. crabs	% occurrence	$\bar{x}$/trawl
41°N, 72°W	2	0	0	0.0	0.00
41°N, 71°W	187	0	0	0.0	0.00
41°N, 70°W	181	3	10	1.6	0.06
40°N, 74°W	13	4	9	30.8	0.69
40°N, 73°W	396	122	355	30.8	0.90
40°N, 72°W	399	39	72	9.8	0.18
40°N, 71°W	318	0	0	0.0	0.00
40°N, 70°W	303	0	0	0.0	0.00
39°N, 74°W	269	134	999	49.8	3.71
39°N, 73°W	250	5	9	2.0	0.04
39°N, 72°W	255	0	0	0.0	0.00
39°N, 71°W	61	0	0	0.0	0.00
39°N, 70°W	23	0	0	0.0	0.00
38°N, 75°W	92	74	1,208	80.4	13.13
38°N, 74°W	390	167	1,986	42.8	5.09
38°N, 73°W	233	1	1	0.4	0.04
38°N, 72°W	34	0	0	0.0	0.00
37°N, 75°W	323	174	1,085	53.9	3.36
37°N, 74°W	264	16	21	6.1	0.08
37°N, 73°W	7	0	0	0.0	0.00
36°N, 75°W	297	80	456	26.9	1.54
36°N, 74°W	183	17	54	9.3	0.29
35°N, 76°W	2	1	1	50.0	0.50
35°N, 75°W	247	77	413	31.2	1.67
35°N, 74°W	78	31	234	39.7	3.00
34°N, 77°W	102	4	4	3.9	0.04
34°N, 76°W	218	30	114	13.8	0.52
34°N, 75°W	75	3	3	4.0	0.04
33°N, 77°W	144	1	1	0.7	0.01
33°N, 76°W	58	0	0	0.0	0.00

NOTES

ANALYSIS OF SEA TURTLE CAPTURES AND MORTALITIES DURING COMMERCIAL SHRIMP TRAWLING

Five species of sea turtles occur in coastal United States waters of the southern North Atlantic and the Gulf of Mexico and are listed and protected under the Endangered Species Act (1973). These are the Kemp's ridley turtle, *Lepidochelys kempi*; hawksbill turtle, *Eretmochelys imbricata*; leatherback turtle, *Dermochelys coriacea*; green turtle, *Chelonia mydas*; and loggerhead turtle, *Caretta caretta*. Each of these species are captured by commercial shrimp trawlers, and these incidental captures have been identified as a source of sea turtle mortalities (Hopkins and Richardson 1984).

Several prior studies have attempted to quantify turtle catch rates and mortalities by trawlers through interviews with vessel captains (Anonymous 1976,[1] 1977[2]; Cox and Mauerman 1976; Rabalais and Rabalais 1980) and through direct observations by observers during commercial shrimp trawling (Hillestad et al. 1978; Ulrich 1978[3]; Roithmayr and Henwood 1982[4]). While these studies provide estimates of capture and mortality rates, more specific information is required to effectively protect the stocks. In particular, managers need to know when and where turtle captures occur, which species are impacted, at what depths the majority of captures occur, and how many turtles are captured and killed.

This report provides a preliminary analysis of existing data collected by fisheries observers during commercial U.S. shrimp trawling. Data from three National Marine Fisheries Service (NMFS) observer projects were used for analysis of turtle catch per unit effort (CPUE) and mortality rates. A brief description of the projects follow:

1) The sea turtle incidental catch and mortality project was instituted to provide information on the incidental capture and associated mortality of sea turtles off the southeastern United States. Trained fishery observers were placed aboard commercial shrimp vessels operating on the major grounds in the Gulf of Mexico and southern North Atlantic from 1979 through 1981.
2) The goal of the excluder trawl project was to design an apparatus for use with existing shrimping gear which would effectively prevent the incidental capture of sea turtles. Initial design and testing of prototype models were conducted during 1977, and field trials were continued through 1984. Fishery observers aboard cooperative and chartered shrimp trawlers began data collection in 1978. Data collection procedures were similar to those of the incidental catch project except that data records were maintained for each net. In this manner, the performance of excluder nets could be compared with that of standard trawls.
3) The objectives of the shrimp fleet discards project were to estimate the magnitude and species composition of incidental fish captures by the Gulf shrimp fleet. Data were collected through contractual arrangements with state agencies from 1973 through 1978. These agencies placed observers on commercial vessels to obtain at-sea sampling off their respective coasts. Data records similar to those of the other two projects were completed for each tow.

In estimating turtle CPUE and mortalities by species, we restricted our analyses to loggerhead, Kemp's ridley, and green turtles. Leatherback and hawksbill turtles were also captured in shrimp trawls, but the infrequency of captures made predictions of CPUE for these species imprecise. In predictions of CPUE for all species combined, these capture records were included.

Data Analyses

For estimations of turtle CPUE and mortalities, the three observer projects were merged. For each data set, effort (E) was standardized to re-

[1]Anonymous. 1976. Incidental capture of sea turtles by shrimp fishermen in Florida. Preliminary report of the Florida West Coast Survey, University of Florida Marine Advisory Program, 3 p.

[2]Anonymous. 1977. Alabama shrimp fishermen interviews for 1977-1978. Marine Resources Office, Alabama Cooperative Extension Service, 1 p.

[3]Ulrich, G. F. 1978. Incidental catch of loggerhead turtles by South Carolina commercial fisheries. Report of the National Marine Fisheries Service, Contract No. 03-7-042-35151, 33 p.

[4]Roithmayr, C., and T. Henwood. 1982. Incidental catch and mortality report. Final report to Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, 20 p.

flect hours towed with a single, 30.5 m headrope length net using the formula

$$E = (\text{nets} * \text{length} = 30.5\text{ m}) * (\text{min} = 60)$$

where nets = number of nets towed,
length = headrope length of a net (meters),
min = minutes fished.

Turtle CPUE ($\hat{R}$) and 95% confidence interval (C.I.) were calculated according to methods described in Snedecor and Cochran (1967) using the formulae

$$\hat{R} = \sum_{i=1}^{n} T_i \Big/ \sum_{i=1}^{n} E_i$$

95% C.I. on $R = \hat{R} + 1.96\,(1/\overline{E})$

$$\sqrt{\sum_{i=1}^{n} (T_i - RE_i)^2/n(n-1)}$$

where R = CPUE (turtles/30.5 m net hour),
$\hat{R}$ = estimated CPUE,
T_i = number of individuals (turtles),
E_i = effort (30.5 m net hour),
n = sample size (number of tows).

The data were stratified by species, season, depth, and statistical zone (corresponding to those used by NMFS for reporting shrimp landings). For each zone, turtle CPUE, mean depth of capture, mean length of tow, and mortality were computed. In summarizing the data, the Gulf of Mexico was subdivided into eastern (NMFS statistical zones 1-7, corresponding to the Florida west coast excluding the panhandle), central (NMFS statistical zones 8-17, corresponding to the Florida panhandle through Louisiana), and western (NMFS statistical zones 18-21, corresponding to the Texas coast) areas. The southern North Atlantic area included the east coast of the United States from Florida to North Carolina, statistical zones 24-33. Part of zone 28, the Cape Canaveral ship channel and adjacent shrimping grounds (lat. 28°15′N to 28°30′N) was excluded to avoid positively biasing CPUE estimates. This habitat harbors large concentrations of turtles throughout the year, and high turtle catch rates (0.3643 ± 0.0045 turtles/hour)[5] do not reflect those occurring on the shrimping grounds outside the Canaveral area. Exclusion of these data is not expected to cause an underestimate of mortalities for the southern North Atlantic because commercial shrimping effort near Cape Canaveral is restricted to three or four vessels during most of the year.

Estimates of shrimp fishing effort for the offshore Gulf of Mexico shrimp fishery were obtained from the NMFS Galveston Laboratory (E. Klima[6]). The shrimp fishing effort was corrected for relative amounts of effort by single rigged, double rigged, and quad rigged vessels and then standardized to 30.5 m net hours. The Atlantic shrimp fishing effort was based on an effort estimate developed in 1983 (Anonymous 1983[7]). Because the data were being updated, more current Atlantic shrimp fishing effort data will be available at a later time.

Percent mortality of the total catch was estimated by a least squares linear regression using percent mortality as dependent upon minutes fished which yielded the relationship of $Y = 0.00165X - 0.03$. The average mortality over 30-min increments of tow length was calculated, and 10 unweighted means were regressed on minutes fished. Although this approach may violate the assumption of homogeneity in regression, it was assumed to be the most appropriate means of describing this relationship, since the dependence of mortality on tow time is strongly statistically significant ($r = 0.98$; $P < 0.001$). Percent mortality was multiplied by turtle captures ±95% upper and lower confidence bounds of turtle captures to estimate the number of turtles killed.

Results and Discussion

Turtle captures and mortality by statistical zone and season with associated trawling effort data were analyzed. While the total observer effort in the Gulf of Mexico (16,771 hours) was greater than the southern North Atlantic (9,943 hours), 482 turtles were captured in the southern North Atlantic and only 52 were captured in the

[5]Means ± the 95% confidence interval will be used throughout the paper.

[6]E. Klima, Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550, pers. commun. Summer 1986.

[7]Anonymous. 1983. Environmental assessment of a program to reduce the incidental take of sea turtles by the commercial shrimp fishery in the southeast United States. U.S. Department of Commerce, National Marine Fisheries Service, 9450 Koger Blvd., St. Petersburg, FL 33702.

Gulf of Mexico (Table 1). This indicates that per unit effort, 16 turtles were captured in the Atlantic for every one turtle captured in the Gulf.

An attempt was made to compare mean depth and duration of tow for turtle captures with the mean depth and duration of tow for all effort by area with and without turtle captures. The mean depth of fishing and mean length of tow were computed from effort data for each statistical zone and for tows in which loggerhead, Kemp's ridley, or green turtles were captured. In most cases (particularly the Gulf of Mexico) sample sizes were small, and no patterns or consistency were evident. We suggest that despite some apparent statistical differences which we attribute to small sample sizes, average depth and tow duration of turtle captures were probably not different from that of the effort.

Summary information on observer effort, CPUE, shrimping effort, estimated captures, and estimated mortality in the Gulf of Mexico and southern North Atlantic are presented for loggerhead, Kemp's ridley, and green turtles (Table 1). Estimated CPUE for all turtles in the Gulf of Mexico (zones 1-21) was 0.0031 ± 0.0008 turtles/net hour, and CPUE for the southern North Atlantic (zones 24-33) was 0.0487 ± 0.0041 turtles/net hour.

The calculation of estimated mortality used minutes fished as a means of estimating the percent of the turtles captured that are killed. Based on mean tow times from our effort data, the overall mortality rate for the Gulf of Mexico is 29%. The eastern Gulf mortality rate is 34%, the central Gulf rate is 22%, and the western Gulf rate is 38%. For the Atlantic coast, the rate is 21% reflecting the shorter average duration of trawl tows on this coast.

The mortality rates based on minutes fished do not distinguish among species. This is because of the small numbers of captures for species other than loggerhead turtles. If there are differences in the ability of the other turtle species to survive long periods of immersion and the stress involved in being captured in a trawl, the differences are not measurable from these data.

In using minutes fished to estimate mortality, the data did not conform to expected models over the range of our observations. In tows of <60-min duration, mortality rates were <1% suggesting that the logistic model might be most appropriate to describe the relationship. However, of logistic, 2d and 3d order polynomial and linear models, the best fit over the range of tow times observed in these studies was provided by the linear model. In tows of <60-min duration and in tows longer than 360 minutes, the linear model is probably inappropriate; mortality is negligible in very

TABLE 1.—Observer effort, turtle captures, CPUE, shrimping effort, estimated captures and estimated mortality of loggerhead, Kemp's ridley, and green turtles in the Gulf of Mexico and the southern North Atlantic.

Area	NMFS observer effort (net hours)	Number of turtles	CPUE ± 95% C.I. on CPUE (turtles/net hour)	Annual shrimping effort (net hours)[1]	Estimated captures (turtles/yr)	Estimated mortality (turtles/yr)
Loggerhead turtles, *Caretta caretta*						
Atlantic	9,943	453	0.0456 ± 0.0039	704,376	32,120 ± 2,747	6,745 ± 577
Gulf of Mexico						
eastern	2,589	12	0.0046 ± 0.0026	611,530	2,813 ± 1,590	956 ± 541
central	6,353	14	0.0022 ± 0.0012	2,391,498	5,261 ± 2,870	1,157 ± 631
western	7,829	16	0.0020 ± 0.0010	1,312,670	2,625 ± 1,313	998 ± 499
overall	16,771	42	0.0025 ± 0.0008	4,315,698	10,789 ± 3,453	3,129 ± 1,001
Kemp's ridley turtles, *Lepidochelys kempi*						
Atlantic	9,943	18	0.0018 ± 0.0008	704,376	1,268 ± 564	266 ± 119
Gulf of Mexico						
eastern	2,589	0	0	611,530	[2]245 ± 245	83 ± 83
central	6,353	2	0.0003 ± 0.0004	2,391,498	717 ± 957	158 ± 210
western	7,829	4	0.0005 ± 0.0005	1,312,670	656 ± 656	249 ± 249
overall	16,771	6	0.0004 ± 0.0004	4,315,698	1,726 ± 1,726	501 ± 501
Green turtle, *Chelonia mydas*						
Atlantic	9,943	7	0.0007 ± 0.0003	704,376	493 ± 211	104 ± 44
Gulf of Mexico						
eastern	2,589	0	0	611,530	[2]61 ± 122	21 ± 41
central	6,353	2	0.0003 ± 0.0003	2,391,498	717 ± 717	158 ± 158
western	7,829	0	0	1,312,670	[2]131 ± 262	50 ± 100
overall	16,771	2	0.0001 ± 0.0002	4,315,698	432 ± 863	125 ± 250

[1]Gulf of Mexcio effort estimates provided by NMFS, Galveston Laboratories (E. Klima text footnote 5) and southern North Atlantic effort based on estimates from Anonymous 1983.
[2]Based on CPUE for the overall Gulf of Mexico.

short tows and never reaches 100% because turtles may be captured at any time during the tow and will survive if captured in the latter stages. Tows shorter than 1 hour and longer than 6 hours, however, are relatively uncommon in commercial shrimping operations.

In the southern North Atlantic, the CPUE for all turtles was strongly dependent on depth (Fig. 1). In depths >10 fathoms, turtle captures were rare, even though, based on aerial surveys (Fritts et al. 1983), turtles are distributed well offshore in waters considerably deeper than 10 fathoms. The strong depth dependency of CPUE may reflect the fact that the continental shelf is relatively narrow along the southeastern seaboard, and the fact that most shrimping occurs in waters <10 fathoms. In the Gulf of Mexico, CPUE appeared to be relatively constant over all depths (Fig. 1).

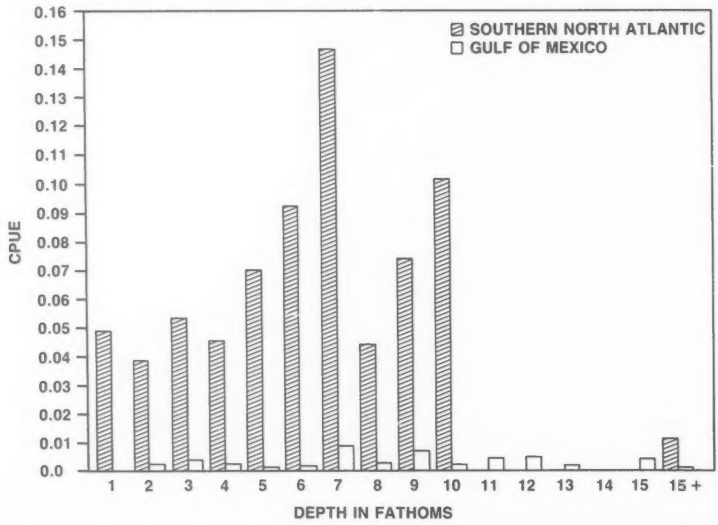

FIGURE 1.—Catch per unit effort (turtles/net hour) as a function of depth for captures in the southern North Atlantic and the Gulf of Mexico.

Conclusions

From our analyses, it is evident that significant numbers of sea turtles are captured by commercial trawlers in both the Gulf of Mexico and the southern North Atlantic, and that over 20% of these turtles are drowned in the trawl. We estimate that 9,874 loggerhead, 767 Kemp's ridley, and 229 green turtles may be killed annually. These estimates are conservative because only offshore (outside the barrier islands) effort and turtle captures were considered.

It should be emphasized that trawl related turtle mortalities are not confined to U.S. waters, but occur on a worldwide basis. The same turtle populations impacted in U.S. waters are also impacted in territorial waters of other countries. In the case of the Kemp's ridley which is believed to be equally distributed in United States and Mexican waters, Mexican trawlers may account for mortalities similar to those of U.S. trawlers. To effectively protect sea turtles, international cooperation is essential.

Acknowledgments

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TYRRELL A. HENWOOD
WARREN E. STUNTZ

National Marine Fisheries Service, NOAA
Southeast Fisheries Center
Mississippi Laboratories
Pascagoula Facility
Pascagoula, MS 39568-1207

THE RELATIONSHIP BETWEEN LUNAR PHASE AND GULF BUTTERFISH, *PEPRILUS BURTI*, CATCH RATE

Through the joint efforts of Japan and the United States, a research program was conducted in fall 1984 and spring 1985 to identify squid resources in the northern Gulf of Mexico (Grace 1984, 1985). Although large concentrations of squid were not located, commercial quantities of gulf butterfish, *Peprilus burti*, were encountered. Maximum sustainable yield (MSY) estimates from the spring data indicated annual potential catches of 50,000 t with a projected ex-vessel value of $19 million (Gledhill[1]). Although gulf butterfish are sufficiently abundant to support a fishery, critical gaps of information on gulf butterfish distribution and location exist which are needed in order to harvest this resource efficiently. Preliminary data from the U.S.-Japan joint surveys indicated that gulf butterfish catch rates were greatest at bottom temperatures of 15°-19°C. Subsequent scientific and commercial efforts at targeting gulf butterfish based upon bottom temperature have produced catches ranging from few individuals to many tons. In a recent study, we found that fishing success for gulf butterfish was often high for several days followed by periods of low success (Allen et al. 1986). This phenomena parallels catch patterns encountered by east coast gulf butterfish fishermen (Amos[2]), who suggest that lunar phase affects catch rates. We analyzed the effect of lunar phase on catch rates. The purpose of this paper is to present evidence that bottom trawling success for gulf butterfish is related to lunar phase.

Methods

Gulf butterfish catches from the two U.S.-Japanese joint surveys and from an additional gulf butterfish survey conducted by SEAMAP (August 1985) were examined. Initially, catch rates per hour of individual trawls were calculated per calendar day. A lunar day value (1-29) was assigned to each calendar day of trawling during the three cruises. Lunar day 1 was assigned to the third calendar day proceeding the new moon on through day 29 falling on the third calendar day following the last quarter moon phase. Mean catch (kg/hour per lunar day) was then calculated and plotted. Catches from trawled stations outside of the depth range in which gulf butterfish were caught during each trip (i.e., < minimum depth or > maximum depth) were not included when calculating mean catch/hour per lunar day.

The effects of moon phase and trip on natural log catch rates ($\ln(x + 1)$, where x = kg/hour per individual trawl) of gulf butterfish were investigated, using the general linear model (GLM) procedures (SAS) Institute (1982). Type III sums of squares were used for the analysis due to unequal number of observations in each subclass. Each observation from each trip was assigned into a lunar phase period (1-4). Mean catch ($\ln(x + 1)$/hour) and number of trawls sampled during each trip and lunar phase are presented in Table 1. An

[1]Gledhill, C. T. 1985. A preliminary estimate of gulf butterfish (*Peprilus burti*) MSY and economic yield. Unpubl. manuscr., 66 p. Southeast Fisheries Center, Mississippi Laboratories, National Marine Fisheries Service, NOAA, Pascagoula, MS 39568-1207.

[2]Duncan Amos, Georgia Marine Extension Program, P.O. Box Z, Brunswick, GA 31523, pers. commun. July 1986.

TABLE 1.—Mean catch ($\ln(x + 1)$/hour) of gulf butterfish and number of trawls sampled during each trip and lunar phase.

Trip	Phase	Number	Mean catch
1	1	6	1.13
1	2	24	2.57
1	3	13	1.58
1	4	31	2.31
2	1	24	2.07
2	2	47	3.24
2	3	9	1.29
2	4	21	2.16
3	1	39	0.49
3	2	35	0.58
3	3	21	0.26
3	4	62	0.40

analysis of variance (ANOVA) model was developed to test for the effect of trip, lunar phase, and the interaction between trip and lunar phase. Scheffe's test was used to contrast each lunar phase with the other three phases.

Results

Peak catch rate was observed to occur in the first quarter moon phase following the new moon (Fig. 1). There was a highly significant difference among trips and lunar phases (Model 1, Table 2). The interaction between trip and lunar phase was not significant ($P = 0.33$) and was therefore dropped from the model resulting in Model 2 (Table 3). In model 2, there was a highly significant difference among trips and a significant difference among lunar phases. A comparison of means using Scheffe's test for each moon phase (Table 4) indicated that catch rate during the first quarter moon phase was significantly greater than catch rates during the last quarter, new, and full moon phases.

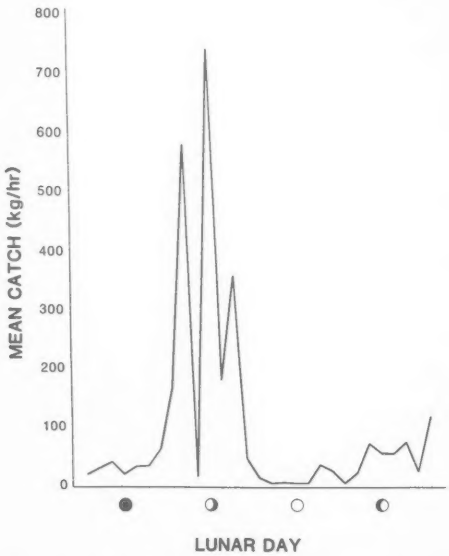

FIGURE 1.—Graph of mean catch (kg/hour) of gulf butterfish by lunar day.

TABLE 2.—Analysis of variance table testing the effects of moon phase (M), research trip (T), and the interaction between trip and moon phase (T * M) on gulf butterfish catch rates during three butterfish research surveys in the Gulf of Mexico 1984-85.

		MODEL 1		
Source	df	ss	*F*-ratio	Pr > *F*
Model	11	384.864	9.90	0.0001**
Error	320	1,130.662		
		TYPE III		
Variable	df	ss	*F*-ratio	Pr > *F*
T	2	175.758	24.87	0.0001**
M	3	43.110	4.07	0.0074**
T * M	6	24.353	1.15	0.3338

**Significant effect at $P < 0.01$.

TABLE 3.—Analysis of variance table testing the effects of moon phase (M) and research trip (T) on gulf butterfish catch rates during three butterfish research surveys in the Gulf of Mexico 1984-85.

		MODEL 2		
Source	df	ss	*F*-ratio	Pr > *F*
Model	5	360.511	20.35	0.0001**
Error	326	1,155.016		
		TYPE III		
Variable	df	ss	*F*-ratio	Pr > *F*
T	2	272.183	38.41	0.0001**
M	3	37.648	3.54	0.0149*

**Significant effect at $P < 0.01$.
*Significant effect at $P < 0.05$.

TABLE 4.—Mean catch rate per hour ($\ln(x + 1)$/hour) by lunar phase

Lunar phase	Catch rate/hour
New Moon	1.09
First Quarter	2.21*
Full Moon	0.88
Last Quarter	1.24

*$P < 0.05$.

Discussion

Although lunar rhythmicity in marine organisms, particularly marine invertebrates, has long been recognized (Palmer 1974), lunar rhythms in which a single peak of activity occurs each month in fishes appear to be rare (Gibson 1978). Most accounts of variations in catch rate of commercially important species which correlate with moon phase refer to clupeids (Gibson 1978). Blaxter and Holliday (1963) suggested several possible explanations for the apparent lunar rhythmicity of clupeid catches including: 1) intensity of moonlight, 2) effect of tides, and 3) fishermen behavior.

Gulf butterfish are normally trawled during daylight when they concentrate near bottom following nocturnal vertical migration. However, this migration is difficult to describe because conventional echo sounding equipment poorly tracks gulf butterfish movement owing to atrophy of the swim bladder in gulf butterfish over 100 mm standard length (Horn 1970). Differences in catch rates between lunar phases may be attributed to changing vertical movements of gulf butterfish in the water column. The lunar pattern is probably not due to onshore-offshore movement out of the fishery's area of operation. In the three research cruises, sampling was stratified by bottom depth (36-585 m) and data do not suggest horizontal movements of gulf butterfish outside these depths.

In conclusion, further work on lunar rhythmicity relationships of gulf butterfish is needed. Results may greatly enhance commercial and scientific efforts in harvesting and surveying gulf butterfish, respectively, by identifying alternate fishing methods (e.g., midwater trawling) that successfully target gulf butterfish during all moon phases.

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JEFFREY H. RENDER
ROBERT L. ALLEN

Coastal Fisheries Institute
Louisiana State University
Baton Rouge, LA 70803-7503

MOVEMENTS OF COHO, *ONCORHYNCHUS KISUTCH*, AND CHINOOK, *O. TSHAWYTSCHA*, SALMON TAGGED AT SEA OFF OREGON, WASHINGTON, AND VANCOUVER ISLAND DURING THE SUMMERS 1982-85

Knowledge of the migration patterns of salmonids in the ocean is an important consideration in developing fishery management plans. Catches of coded-wire tagged salmon in the ocean have yielded much information on general distribution patterns of different stocks and species of salmon (see for example Hunter [1985], Garrison [1985], and Howell et al. [1985]). Other studies have dealt with movements of salmon tagged in offshore waters of the northern North Pacific Ocean (Hartt 1962, 1966; French et al. 1975; Godfrey 1965; Godfrey et al. 1975) and in coastal waters of British Columbia, Washinton, Oregon, and California (Milne 1957; Vernon et al. 1964; Kauffman 1951; Van Hyning 1951; Fry and Hughes 1951). Movements of juvenile salmon in coastal waters of the Gulf of Alaska were studied by Hartt and Dell (1986); in Georgia Strait, British Columbia, by Healey (1980); and in coastal waters off Oregon and Washington by Pearcy and Fisher (unpubl. manuscr.)[1].

[1]W. C. Pearcy and J. P. Fisher. Migration of coho salmon (*Oncorhynchus kisutch*) during their first summer in the oceans. Unpubl. manuscr. College of Oceanography Oregon State University, Corvallis, OR 97331.

Movements of individual maturing salmon off Oregon and Washington are still poorly known. In this paper we examine migration after tagging of salmonids collected during purse seine cruises off the Oregon and Washington coasts from 1982 to 1985 and off the west coast of Vancouver Island, B.C., in 1984.

Methods

Maturing and juvenile salmon were collected by purse seine during May 1982, 1983, and 1985; June 1982-85; July 1984; and September 1982-84. Coho salmon, *Oncorhynchus kisutch*, were classified as maturing or juvenile, based on the length-frequency distribution of the catch in each month. The distribution was usually bimodal and the division between juvenile and maturing coho salmon was about 300 mm FL in May and June, 360 mm FL in July, and 420 mm FL in August and September. Chinook salmon, *O. tshawytscha*, ≤400 mm in all months were arbitrarily classified as juveniles.

Numbered orange Floy[2] tags were applied with a Dennison Mark II tagging gun between the pterygiophores just below the dorsal fin of fish anesthetized with MS-222. Fish were allowed to recover for a few minutes in tanks with circulating saltwater and then were released into the ocean. Date and location of release was recorded for each tagged fish. Condition of the fish after handling varied, but most swam vigorously in the recovery tank and rapidly swam away when released. However, some scale loss almost always occurred and for some individuals was extensive.

Information on movements of coho and chinook salmon was obtained from subsequent recoveries in ocean and terminal fisheries and on spawning grounds or at hatcheries. No reward was offered

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of mark and recovery data for coho and chinook salmon tagged in the ocean off Oregon, Washington, and the west coast of Vancouver Island.

	Maturing coho		Juvenile coho		Maturing chinook		Juvenile chinook	
Year	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)
1982	194	21 (10.8)	0	—	73	3 (4.1)	0	—
1983	142	17 (12.0)	0	—	5	1 (20.0)	0	—
1984	162	10 (6.2)	86	3 (3.5)	56	4 (7.1)	27	0 (0)
1985	215	13 (6.0)	18	0 (0)	37	8 (21.6)	46	1 (2.1)
All years	713	61 (8.6)	104	3 (2.9)	171	16 (9.4)	73	1 (1.4)

	Maturing coho		Maturing chinook	
Other studies:	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)
Fry and Hughes (1951) Tagging off California in 1939-42, 1948, 1949	954	26 (2.7)	6,144	483 (7.9)
Boydston (unpubl.) Tagging off California in 1971 and 1972	3,341	409 (12.2)		
Van Hyning (1951) Tagging off Oregon in 1948 and 1949	506	29 (5.7)	221	11 (5.0)
Kauffman (1951) Tagging off Washington and W. coast Vancouver Is. in 1948 and 1949	65	16 (24.6)	635	33 (5.2)
Milne (1957)	5,458	476 (8.7)	7,194	970 (13.5)

for return of tags. The straight line distance between release and recovery locations indicated the minimum distance travelled (called "net movement") for fish recovered in the ocean. A series of connected straight line tracks were used to estimate net movement of fish recovered in locations where a single line could not be used (e.g., recoveries in Puget Sound). Straight line distance travelled in the ocean was added to distance travelled upstream to estimate net movement for fish recovered in river systems. Approximate latitudinal change was used to estimate net movement of fish for which an accurate recovery location was not known (e.g., "recovered off Coos Bay"). Net migration rate was estimated by dividing net movement by days between release and recovery.

Results and Discussion

Numbers of fish tagged and percentages recovered are summarized in Table 1 for coho and chinook salmon released in different years. Recovery rates were similar for maturing coho (mean 8.6%, range 6-12%) and chinook (mean 9.4%, range 4-22%) salmon. These are similar rates to those found for these two species in other studies (Table 1).

Numbers of fish recovered in different areas from releases off Oregon, Washington, and Vancouver Island are given in Table 2. Simplified migration patterns are shown in Fig. 1. Recoveries of coho salmon released off Oregon were mainly (81%) from the Columbia River and Oregon. Only 11% were recovered in the Strait of Juan de Fuca or Puget Sound. This distribution differs from Van Hyning's (1951) finding that 47% of coho salmon tagged between June and August from Cape Lookout, OR, to the Columbia River were recovered in Puget Sound. Recoveries of coho salmon released off Washington were more widely distributed and 46% were recovered from the Columbia River to Cape Flattery, 20% in Oregon, 23% in the Strait of Juan de Fuca or Puget Sound areas, and 11% in British Columbia.

Estimated net migration of coho salmon between release and recovery (including upstream migration for those recovered in freshwater) averaged 181 km and ranged from 7 to 657 km (Fig. 2A.) Most coho salmon were recovered within 150 days of release. The two fish recoverd after 330 and 380 days were released as juveniles and recovered the following year as adults.

Net migration rates of the maturing coho salmon tagged in coastal waters were generally very low and ranged from 0.1 to 20.4 km/day with a mean rate of 3.6 km/day (Fig. 2B). Coho salmon recovered in the open ocean off Oregon, Washington, or Vancouver Island (circles) had only slightly higher mean rates of movement than those recovered in the Strait of Juan de Fuca or Puget Sound areas (triangles) or those recovered

TABLE 2.—Recovery areas of tagged coho and chinook salmon released off Oregon, Washington, and the west coast of Vancouver Island.

	Recovery areas										
Release areas	Ocean off N. California	Ocean off Oregon	Coastal Oregon bays & rivers	Columbia River	Ocean off Washington	Coastal Washington bays & rivers	Ocean off W. Vancouver Island	Strait of Juan de Fuca	Puget Sound	British Columbia Rivers	Other British Columbia
Coho											
Off Oregon		11	7	3		2		2	1		
Off Washington		6	1	7	8	1	2	3	5	1	1
Off west Vancouver Island							1				
Chinook											
Off Oregon	1	2	2	1	1						
Off Washington		3		3	2					1	
Off west Vancouver Island								2			

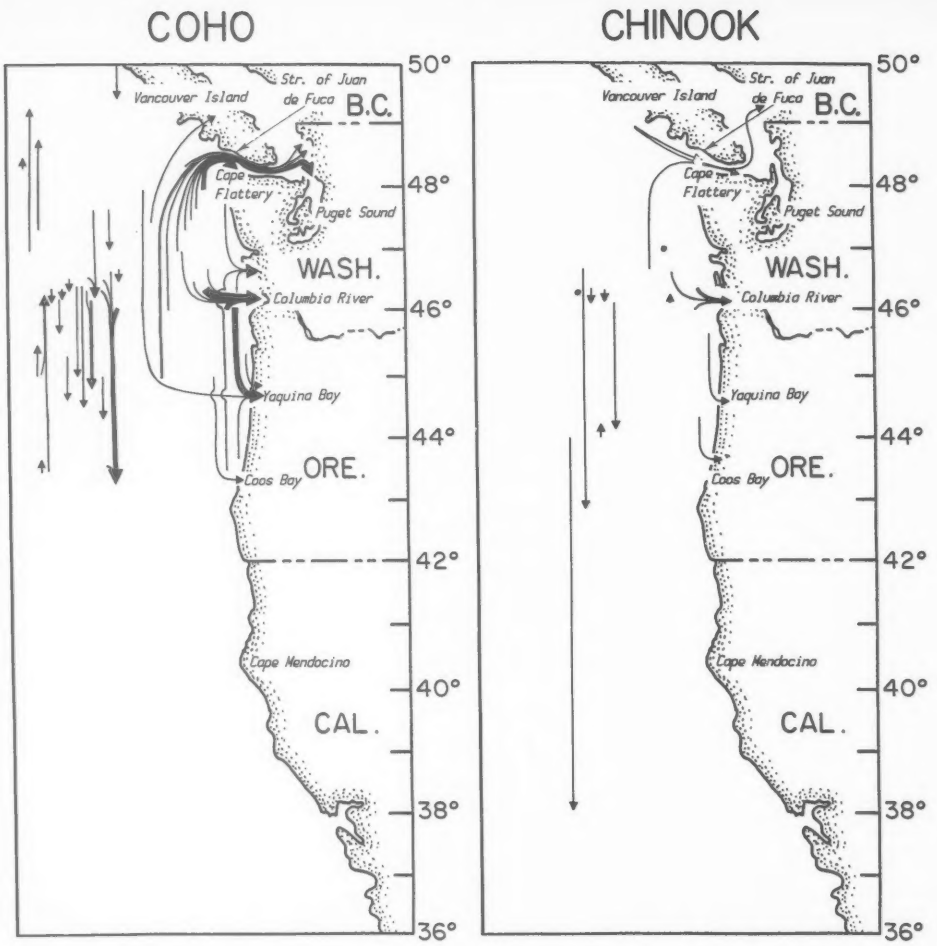

FIGURE 1.—Migration patterns of tagged coho and chinook salmon released at sea. For fish recovered in the ocean off Oregon, Washington, or Vancouver Island, release latitude is indicated by the tail of the arrow and recovery latitude by the head of the arrow. For fish recovered in inland waters or river systems the head of the arrow points to the system in which the fish was recovered. Solid dots indicate fish released and recovered at the same latitude. Numbers of fish are approximately proportional to thickness of arrows. Most releases and recoveries were within 50 km of the coast and the positions of arrows do not represent true distances from shore.

in coastal bays or river systems, including the Columbia River (squares) (4.4, 3.5, and 2.7 km/day, respectively, Fig. 2B). Similar low net movement rates were found for coho salmon in coastal waters by Van Hyning (1951) off Oregon (3.0 km/day), by Kauffman (1951) off Washington and Vancouver Island (3.9 km/day), and by Milne (1957) also off Vancouver Island (9 km/day).

In all studies the stresses related to capture and tagging may cause some mortality and weaken some surviving fish, affecting speed of migration. Hartt (1966) suggested that tagging retards migration by at least 1 day. However, movements of fish immediately after release in sonic tagging experiments were often rapid (Madison et al. 1972; Stasko et al. 1973).

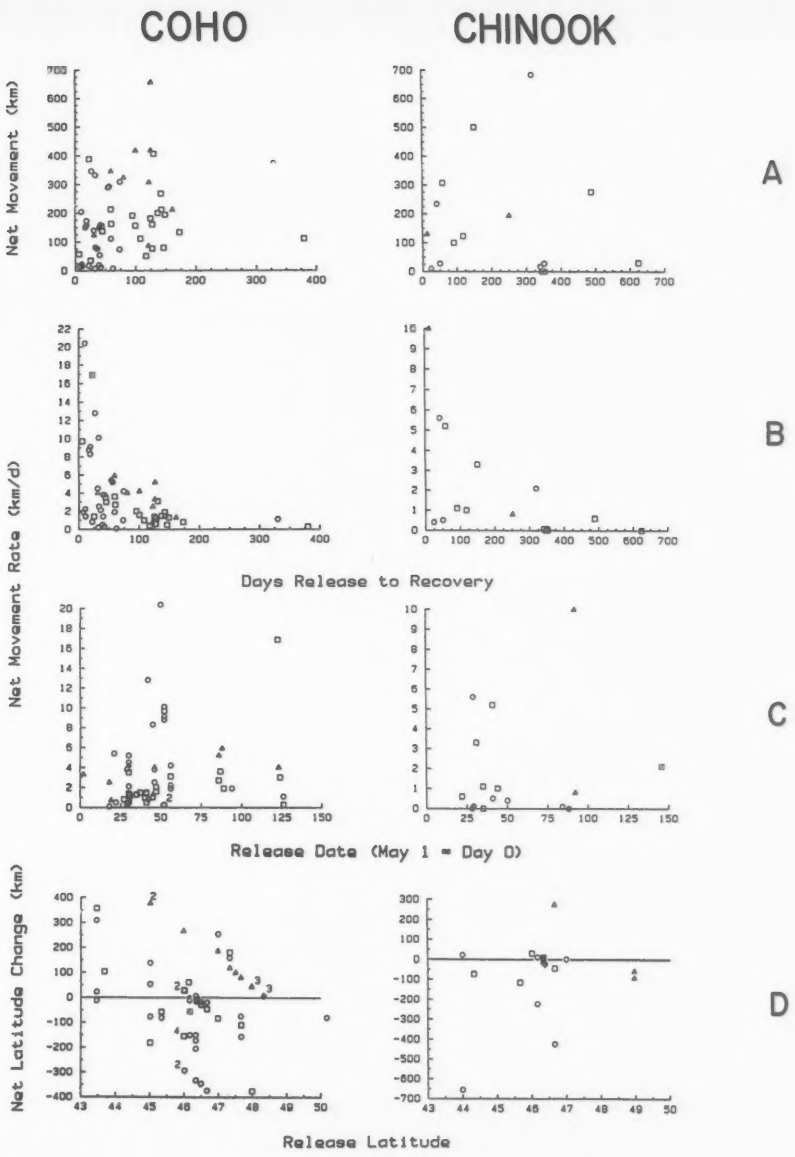

FIGURE 2.—A) net movement vs. days between release and recovery, B) net movement rate vs. days between release and recovery, C) net movement rate vs. release date, and D) net latitude change (+ = north and − = south) vs. release latitude for tagged coho and chinook salmon. Recoveries in inland waters (Strait of Juan de Fuca, Puget Sound, Georgia Strait, and associated river systems) are indicated by triangles, those in the open ocean from the west coast of Vancouver Island to northern California by circles, and those in coastal bays or river systems by squares. For fish released off Oregon or Washington and later recovered in Puget Sound, net latitudinal change (D) is given as the change between the release location and Cape Flattery.

In contrast to the low movement rates observed for coho salmon in coastal waters off Oregon, Washington, and Vancouver Island, net migration rates reported for salmon tagged in offshore waters of the North Pacific were generally much higher. Godfrey et al. (1975) calculated an average rate of 24 km/day for tagged coho salmon recovered in the Japanese high seas fishery and 30 km/day for coho recovered in coastal waters. Hartt (1962, 1966) estimated that the migration rates of sockeye salmon into Bristol Bay averaged 44-50 km/day, whereas those of maturing sockeye salmon caught on the high seas averaged about 32 km/day. Chum salmon had migration rates at sea of 23-50 km/day; pink salmon had average rates of 43 km/day for coastal returns and 50 km/day for high seas returns.

Rapid migrations in coastal waters of British Columbia and Washington were also found for pink salmon (Vernon et al. 1964; Stasko et al. 1973) and for sockeye salmon (Madison et al. 1972) and off the Kurile Islands for chum salmon (Ichihara et al. 1975). However, migration rates slowed greatly as fish neared their home river systems (Vernon et al. 1964; Groot et al. 1975).

Because net migration rates of coho salmon in coastal waters off Oregon, Washington, and Vancouver Island are so much lower than movement rates found for other salmon stocks, these coho are probably spending less time migrating in a single direction compared to meandering and feeding. Similarly, Milne (1957) concluded that coho salmon in coastal waters of British Columbia probably meander during both feeding and spawning migrations. Slow, feeding movements off Oregon and Washington are also suggested by the long time period (3-4 months) during which individual stocks are available in the ocean fisheries (Hunter 1985). The relatively fast net migration rates observed for some coho salmon recaptured within 33 days of release (Fig. 2B) suggest that actual movement rates over short time periods may be quite high but that meandering courses over time produce low net migration rates. Higher migration rates for fish tagged in late summer, to be expected if movements were changing from predominantly feeding to homing, were not apparent (Fig. 2C).

Roughly equal numbers of coho salmon were recovered to the north (27) and to the south (35) of release sites, although most (8 of 11) coho released from lat. 45°N and south were recovered to the north (Fig. 2D). Van Hyning (1951) also found that most coho tagged south of 45°N travelled to the north after release; however, he found that most coho released off northern Oregon and the Columbia River (46°15′N) were recovered to the north as well. Fry et al. (1951) and L.B. Boydston (California Department of Fish and Game, unpubl. data) reported that most recoveries of maturing coho salmon tagged off northern California were to the north, off Oregon or Washington.

Northward migration by most of the maturing coho salmon tagged at sea south of 45°N during their final summer in the ocean is consistent with the distributional patterns of coastal Oregon and early run Columbia River stocks in the ocean fisheries. Peak catches of coastal Oregon coho salmon stocks are off northern California in May and June and shift to waters off Coos Bay in July and August (compiled from Hunter 1985). Relatively high percentages (24-37%) of the ocean catch of coastal Oregon coho salmon stocks (all combined) are off northern California (Garrison 1985; Hunter 1985; Oregon Department of Fish and Wildlife 1982). Similarly, between 62 and 65% of early run Columbia River stocks are caught south of the Columbia River (Hunter 1985; Howell et al. 1985; Oregon Department of Fish and Wildlife 1982). Therefore, many fish from these two stock groups, which make up a substantial fraction of the coho catch off California and Oregon, migrate south and then migrate north sometime later during the summer to return to their natal systems. Southward migration into waters off northern California and southern Oregon may be advantageous to these coho salmon stocks because of the potentially high food production fueled by strong coastal upwelling during the summer in this area.

Other stocks of coho salmon are caught to the north of where they entered the ocean during their final summer in the ocean. About 47% of the late run Columbia River coho are caught north of the Columbia River in Washington and British Columbia (Howell et al. 1985). Smaller, but significant percentages of other stock groups from the south (early Columbia River, private hatchery, and other coastal Oregon groups) are also caught as maturing adults north of their natal streams. Thus, these fish would eventually have to migrate to the south to return to their natal streams. Therefore, the subsequent southward movement of many of the maturing coho salmon we tagged north of 45°N (Fig. 2D) is not surprising.

The slow net migration rates, prolonged residence in coastal waters, and mixed north and

south net movements suggest that maturing coho salmon in coastal waters of Oregon and Washington, unlike stocks of salmon from the Gulf of Alaska and Bering Sea regions, are not highly migratory with precisely directed and timed movements. Many juvenile coho salmon off Oregon and Washington also reside in coastal waters and do not appear to undertake rapid or long migrations out of this region (Pearcy and Fisher fn. 1).

Of the 7 recoveries of chinook salmon released off Oregon, 5 were off Oregon, in the Columbia River, or in coastal Oregon rivers; 1 was off northern California; and 1 was off Washington. Of the 9 recoveries of chinook salmon released off Washington, 3 were in the Columbia River, 3 off Oregon, 2 off Washington, and 1 in British Columbia. Two chinook salmon tagged off the west coast of Vancouver Island were recovered in the Strait of Juan de Fuca (Fig. 1, Table 2).

Estimated net migration of chinook salmon averaged 201 km and ranged from 0 to 685 km (Fig. 2A). Unlike coho salmon, which spend only 1 year in the ocean and which were mostly recovered within 150 days of release, almost half of the chinook salmon, which may spend several years in the ocean, were recovered after more than 200 days at liberty. Mean net migration rate of chinook salmon was 1.9 km/day (n = 16, Fig. 2B). As was found for coho salmon, net migration rates of chinook salmon were many times lower than rates found for salmon tagged in offshore waters of the North Pacific Ocean. Therefore, some chinook salmon also appear to undertake meandering feeding movements in coastal waters off Oregon, Washington, and Vancouver Island. There was no evidence for acceleration of migration rate late in summer (Fig. 1C).

Tagged maturing chinook salmon differed from coho salmon in that most moved to the south after release (Fig. 2D). Columbia River and many coastal Oregon stocks of chinook salmon are caught in the ocean fisheries predominantly to the north of Oregon, i.e., north of their natal systems (Wahle et al. 1981; Garrison 1985). Some of the maturing chinook salmon that we tagged may have been moving slowly toward their natal systems from the north. One chinook salmon was recovered 319 days after release over 656 km to the south, off northern California (Figs. 1, 2D).

Other species of salmonids tagged off Oregon and Washington were recovered only in very low numbers. There were only 2 recoveries from 164 tagged pink and 36 tagged chum salmon. The greatest net movement was by a chum salmon tagged on 1 June 1985 off Seaside, OR, just south of the Columbia River and recovered on 8 August 1985 in Hecate Strait, B.C. (great circle distance 830 km). This fish was at liberty for 68 days and its minimum movement rate as 12.2 km/day.

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J. P. FISHER
W. C. PEARCY

College of Oceanography
Oregon State University
Corvallis, OR 97331

DAILY GROWTH INCREMENTS IN OTOLITHS OF JUVENILE BLACK ROCKFISH, *SEBASTES MELANOPS*: AN EVALUATION OF AUTORADIOGRAPHY AS A NEW METHOD OF VALIDATION

Investigations into the temporal periodicity of growth increment formation in otoliths of larval and juvenile fishes have produced conflicting accounts. Taubert and Coble (1977), Barkman (1978), Wild and Foreman (1980), and Campana and Neilson (1982), among others, have confirmed daily increment formation in otoliths from various species of larval and juvenile fishes. There have been a few studies, however, in which increment counts were not representative of actual age of the fish (Wild and Foreman 1980; Geffen 1982; Neilson and Geen 1982). Nondaily increment formation has been explained by the inclusion of subdaily rings in age estimates as well as by methodological errors in preparing and viewing the otoliths (Campana 1983a; Campana and Neilson 1985). Since size and age of fish, food limitations, and environmental conditions have been suggested to affect increment formation, validation is necessary in each study where fish age is estimated.

Several techniques have been used to validate daily growth increments in larval and juvenile fish otoliths. Fish of known age, raised from fertilization or birth under controlled laboratory conditions, provide the best material to determine frequency of increment formation (Taubert and Coble 1977; Barkman 1978; Tanaka et al. 1981; Miller and Storck 1982). For many species, however, rearing the larvae from birth through the juvenile stage is difficult or impossible. An alternate method of age validation introduces a chemical mark onto those calcified structures which exhibit periodic growth zones, such as otoliths, scales, and spines. The antibiotic oxytetracycline hydrochloride (OTC) has been used most successfully in this manner (Wild and Foreman 1980; Campana and Neilson 1982; Ralston and Miyamoto 1983; Dabrowski and Tsukamoto 1986). The OTC is taken up at the site of calcification and fluoresces bright yellow under ultraviolet light, compared with the blue autofluorescence of normal tissue. Most recently, stable strontium has been used to demonstrate daily increment formation in squid statoliths (Hurley et al. 1985) and in mass marking of coho salmon (Yamada et al. 1979). For some species, a timemark may also be induced on the otolith by stress,

such as cold shock (Mugiya and Muramatsu 1982), or by simply bringing field-captured fish into the laboratory (Boehlert and Yoklavich 1985). Comparing increment counts with number of days following the time-mark accurately estimates frequency of occurrence of the growth increments. Our study evaluates the commonly used OTC and an alternate chemical, the radioisotope calcium-45, in terms of their success as time-markers to validate daily growth increment formation in the otoliths of juvenile black rockfish, *Sebastes melanops*.

Materials and Methods

Young-of-the-year black rockfish, *Sebastes melanops*, ranging from about 2 to 5 g wet body weight and 47 to 64 mm standard length (SL), were collected from a rocky, intertidal area 8 km south of Newport, OR, in July 1982 and from Yaquina Bay, OR, in July 1983. Fish were held in 200 L tanks under ambient water temperature conditions which fluctuated between 13° and 17°C; a ration of ground squid and shrimp was offered ad libitum and photoperiod was maintained at 13 h light and 11 h darkness. After at least 10 days of acclimation to laboratory conditions, fish were anesthetized with MS-222 and injected intramuscularly (midbody below dorsal fin) with a solution of either OTC or calcium-45. Fish continued to feed immediately following injection and handling.

Calcium-45

Fish were injected with a solution of low-calcium physiological saline and calcium-45 ($^{45}CaCl_2$ dissolved in HCl; New England Nuclear).[1] Through preliminary experiments, a dose of 0.1 μCi ^{45}Ca/g wet body weight proved to be optimum for isotope uptake and retention. Four fish each were sacrificed at 1, 4, 12, 24, 48, 72, 96, 120, 144, 168 hours and at subsequent 4-d intervals for 63 days following injection. Three fish were sacrificed after having maintained good health and growth for 1 year following injection. Four nonradioactive fish were sacrificed on the first day of the experiment and used as blanks or controls in determining activity levels of the injected fish.

At the time intervals specified above, fish were anesthetized, blotted dry, measured (nearest mm, SL), and weighed (nearest 0.01 g). Both sagittal otoliths were removed from each fish, rinsed thoroughly in water to remove surface contamination of calcium-45, and stored dry for liquid scintillation counting (LSC) or autoradiography. One otolith from each fish, with the exception of the three 1-yr-olds, was weighed, dissolved in 0.1 mL concentrated HCl, diluted with 10 mL of Beckman Ready-solv EP liquid scintillation cocktail, and assayed for calcium-45 activity in a Beckman LS 8000 liquid scintillation counter. Activity was corrected for decay and quench and expressed as disintegrations per minute (DPM) per mg of sample. The perceived decrease in radioactivity due to the increase in weight of otolith over the experimental period was corrected using the following equation:

$$\text{Corrected activity} = \frac{\text{DPM}}{\text{mg tissue}_{t_f}} \times \frac{\text{weight tissue}_{t_f}}{\text{mean weight tissue}_{t_i}}$$

where t_f is time at sacrifice and t_i is time of experiment initiation. Mean weight of otolith at t_i was obtained from the 4 fish sacrificed prior to injection; since all fish were of similar length at the onset of experimentation, these 4 fish adequately represented size of injected fish.

Four otoliths from time interval 1 hour and two otoliths from each of intervals 4 and 12 hours and 1, 4, 11, 19, 39, 55, and 63 days were prepared for autoradiography. The right otolith of each pair was affixed to a microscope slide with histological mounting medium. The proximal surface of the otolith was ground with 600 grit carborundum paper on a rotating wheel until the focus was just visible and most of the curvature of the otolith was removed. The mounting medium was gently heated and the otolith was turned to expose the distal surface. Grinding was continued until most of the mounting medium was removed from the margins of the otolith. The external surface was polished using jeweler's rouge (3 μm) and the whole slide was immersed in an ultrasonic cleaner to remove all loose particles from the otolith surface. The resulting sagittal section was coated with Kodak NTB3 nuclear emulsion and exposed in a light-tight box for 8 days at 4°C. The autoradiographs were developed in Kodak D-19 developer for 2 minutes, fixed for 5 minutes in

[1]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

Kodak Fixer, rinsed for 20 minutes in distilled water, and viewed under transmitted light with a compound microscope at 400× magnification to determine presence and location of exposed silver grains. Growth increments were enumerated from the time-mark to the otolith margin. In most of the otoliths, a check (or exceptionally dense band) was noted prior to the deposition of the radioactive mark. The location of this check, in terms of numbers of increments from the time-mark, was also determined.

Oxytetracycline

A stock solution was prepared using 25 mg OTC (Sigma Chemicals Co.) in 5 mL of physiological saline. Each fish received a dosage of 0.5 mg OTC or 0.1 mL of stock solution. This approximates the dosage reported by Mugiya and Muramatsu (1982) for goldfish and Weber and Ridgway (1962) for sockeye salmon smolts. Fish were sacrificed 21 days after injection, weighed and measured, and both sagittal otoliths were removed, cleaned, and stored dry in the dark.

A sagittal section of the right otolith was prepared as previously described. Sections were viewed at 160× magnification, using a compound light microscope equipped with ultraviolet illumination. The fluorescent mark was located with an ocular marker. Increments were enumerated from this mark to the outer margins of the otolith using visible light.

Results and Discussion

Calcium-45

One hundred and three black rockfish were injected with the radioisotope, calcium-45; there were no mortalities during the 63-d postinjection sampling period. Over the course of the experiment, average fish length increased from 52.5 mm (SD = 1.29, $N = 4$) on day zero to 70.5 mm (SD = 8.23, $N = 4$) on day 63; average total body weight increased from 2.3 g (SD = 0.13, $N = 4$) to 8.10 g (SD = 2.60, $N = 4$).

LSC demonstrated that calcium-45 was taken up and retained in the sagittal otoliths of all fish. Incorporation of calcium-45 into the otolith occurred as early as 1 hour following injection, which was the initial sampling interval; mean activity at this time was 1,377 (SE = 329) DPM/mg otolith (Fig. 1). Similar activity values and uptake patterns of calcium-45, up to 72 hours

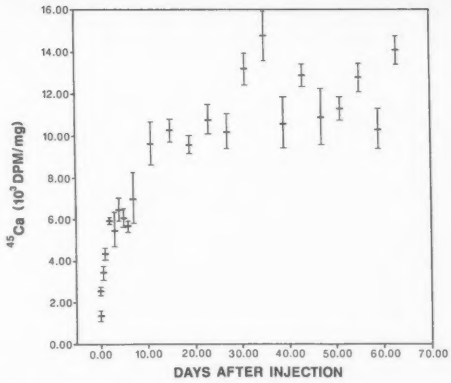

FIGURE 1.—Accumulation and retention of ^{45}Ca in the otolith of black rockfish. Mean activity and 1 SE are indicated. $N = 2$ to 4 fish per time interval.

postinjection, were observed in the otoliths of rainbow trout, although times of maximum incorporation and retention were not assessed over longer periods (Mugiya 1974). Radioactivity in the rockfish otoliths increased sharply for the first 15 days (up to an average of 10,279 DPM/mg, SE = 581), followed by a gradual increase to an apparent asymptote (Fig. 1). The rapid uptake and retention of calcium-45 in liver, muscle, and epidermis of *S. melanops*, and the gradual elimination of the isotope from these tissues (Yoklavich and Boehlert unpubl. data), could contribute to the increase in otolith activity over time; presumably, calcium-45 is transported from these tissues to the otolith via the blood (Mugiya 1974). The lack of decrease in activity in the otolith substantiates the findings of Ichii and Mugiya (1983) and Campana (1983b), which suggest that calcium deposited in otoliths of goldfish and stressed coho salmon, respectively, remains immobilized and is not resorbed. Although no data were presented, it had been suggested earlier by Pannella (1980) that resorption of calcium occurs in the otoliths of some tropical fish species, possibly invalidating ages based on increment counts. Our data show no evidence of resorption, lending support to the usefulness of increment counts in reliably estimating age.

Scattered exposed silver grains were evident along the interface of otolith section and mounting resin in the autoradiographs of otoliths from the earliest sampling periods (1 hour to 1 day), although positive association of the grains with a

distinct site of isotope incorporation into the otolith was not discernible. Since the radioactive mark was on the edge of the otoliths from these early sampling periods, it was more difficult to identify than the mark left on otoliths of fish sacrificed later in the experiment. Distinct bands of silver grains, designating the site of isotope uptake, were evident in all but four otoliths sampled from day 4 through day 63 (Fig. 2). A less dense background of grains spanned 7 to 10 bands around the site of uptake; postinjection increment counts were made from the site of densest grain

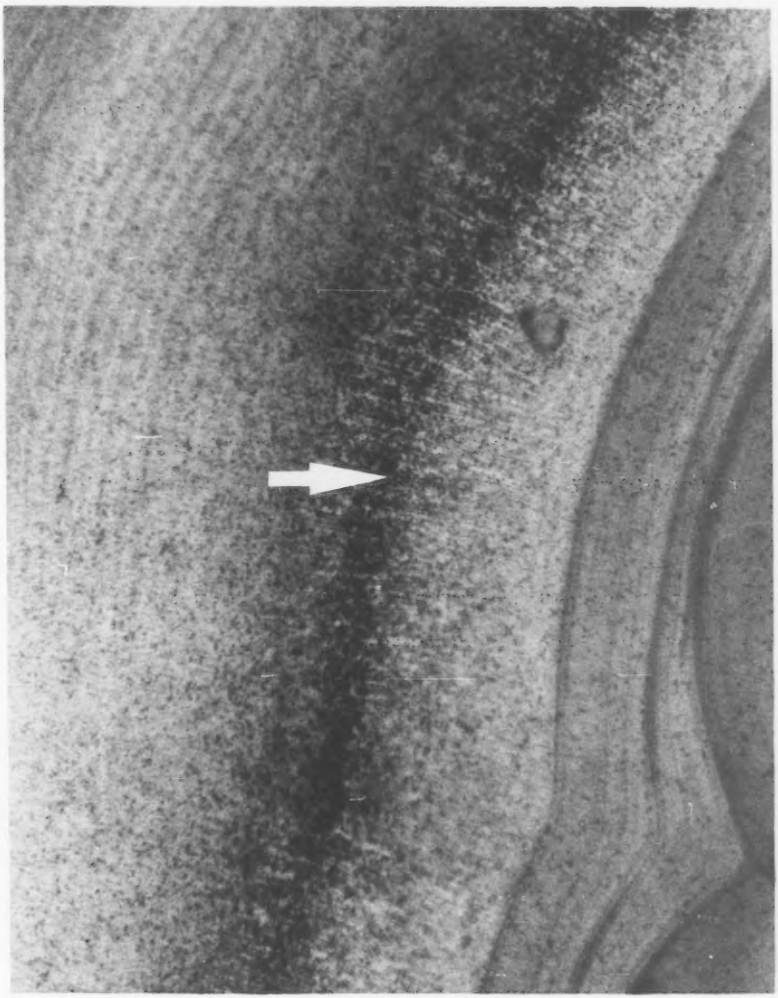

FIGURE 2.—Example of the silver grains produced by the autoradiograph of ^{45}Ca in the otolith of a 69 mm juvenile black rockfish. Arrow indicates band of densest grains; for scale, arrow = 35 μm. This photo is from the anterodorsal region of the otolith. Note the clear increments present on the left side of the figure, representing the increments distal to the time-mark.

accumulation to the edge of the otolith. The posterodorsal area of the sagittal sections showed the heaviest accumulation of the isotope and was also the easiest area in which to count increments. This observation is consistent with Irie (1960) and Mugiya (1974), who concluded that high calcium uptake occurred in the dorsal region, as well as in the anterior and posterior tips of otoliths; these are the regions of fastest otolith growth.

The number of growth increments from the band of densest accumulation of silver grains to the edge of the otolith section closely approximated the number of days the fish were held in the laboratory following injection (Table 1), thereby validating the occurrence of daily growth increments in these juvenile black rockfish. Validation of the frequency of growth increment formation, obtained from fish held under optimal growth conditions in the laboratory, and the apparent lack of otolith resorption, as demonstrated by the increasing retention of calcium-45 with time, suggest that daily increments on otoliths could provide accurate representation of age and growth for field-caught juvenile *Sebastes melanops*. Daily increments have recently been suggested to occur on otoliths of early larvae of *S. marinus* (Penny and Evans 1985). In previous work on juvenile *Sebastes*, growth increments had been counted but not validated (Moser and Ahlstrom 1978; Boehlert 1981). Our study is thus the first confirmation of daily increments on otoliths of juvenile *Sebastes*.

Checks, or exceptionally dense and dark bands deposited as daily increments, were observed in otoliths from fish used in the calcium-45 experiments. One check preceded the radioactive time-mark and another check was associated with the time-mark itself. Ten growth increments were noted from the earliest check to the time-mark in each otolith (Table 1). Formations of checks in otoliths have been documented for many species, including coho salmon (Campana 1983b), goldfish (Mugiya and Muramatsu 1982), and several tropical species (Brothers et al. 1983). Such checks have been attributed to periods of physiological stress to the fish due to collection, migration, change in feeding or habitat, temperature, life history stages, or anything else that disrupts growth. In the present study, the time from fish collection to injection of the isotope marker was 10 days (Table 1). It seems clear that the observed checks were produced as a consequence of stress encountered during capture and transport to laboratory conditions and can be used as additional evidence of daily deposition of growth increments. If such checks are reliably produced, they may be better than chemical time-markers for validation studies such as these.

TABLE 1.—Age validation using otoliths from black rockfish marked with calcium-45 or oxytetracycline. Number of days from capture to injection is compared with number of growth increments from capture check to time-mark; number of days from injection to sacrifice is compared with number of increments from time-mark to margin of otolith.

Treatment/ sample size	Number of days from		Mean number increments from	
	Capture-injection	Injection-sacrifice	Check-mark	Mark-margin
^{45}Ca/4	10	0.04	10	[1]0
/2	10	0.17	10	[1]0
/2	10	0.5	10	[1]0
/2	10	1	10	[1]0
/1	10	4	10	4
/1	10	11	10	11
/1	10	19	10	19
/2	10	39	10	36
/1	10	55	10	55
/2	10	63	10	63
OTC /5		21		21

[1]Scattered silver grains associated with margin.

Oxytetracycline

The OTC was incorporated into the otoliths of each of the 15 fish injected and produced a distinct fluorescent band. The growth increments following injection of OTC, however, were less distinct on most of the otoliths and consequently all otoliths could not be used to validate daily increment formation. Weak increment definition following OTC incorporation in otoliths of larval spot and pinfish has been reported by Hettler (1984). Although Hettler suggested that the lack of distinct increments resulted from experimental stress, postinjection increments were clearly visible in otoliths from the juvenile rockfish which were injected with calcium-45 and held under laboratory conditions similar to the OTC experiments. Five of the rockfish otoliths did display clear growth bands following the fluorescent time-mark; enumeration of these increments is summarized in Table 1. These otoliths show the same results as those from calcium-45 treatments, demonstrating the daily periodicity of growth increment formation in juvenile black rockfish. It is unclear, however, why 67% of the otoliths failed to produce prominent daily increments after OTC incorporation.

The fluorescent OTC mark was more intense

and easier to identify than the exposed silver grains in the autoradiographs of most otoliths. OTC is less hazardous to handle in the laboratory and can be detected in the otolith for much longer periods than calcium-45. The OTC was still visible in the otolith at least 3 years following injection and has in fact been used in studies for mass-marking of fish for identification purposes, where time at liberty may be even longer (Tsukamoto 1985). The activity of calcium-45 was evident in autoradiographs of a few otoliths which were developed 2 years following injection; amount of activity depends upon the effective half-life of the isotope (164 days for calcium-45) and the initial amount of activity in the tissue. An autoradiograph of a transverse section through the otolith of one of the fish injected and held for 1 year revealed a discontinuous band of very faint, exposed silver grains, dispersed primarily over the internal and dorsal areas of the otolith. Association of the isotope with an annular band was not observed. Autoradiographs are difficult to produce, expensive, and time consuming. On the other hand, OTC is simply observed in the otolith section under ultraviolet light. Our recommendations for validating the daily formation of growth increments in juvenile rockfishes are 1) the use of OTC, if growth increments can be routinely identified following injection, or 2) stress marks, which are induced either when transferring fish from the field to laboratory or by subjecting fish to abrupt environmental changes. Where this type of induced stress is not appropriate, as in environmentally controlled laboratory studies, and OTC marking is unsuccessful, marks could reliably be produced with the calcium-45 technique described in this paper.

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Mary M. Yoklavich

Mark O. Hatfield Marine Science Center
Oregon State University
Newport, OR 97365
Present address: *Northwest and Alaska Fisheries Center*
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, BIN C15700
Seattle, WA 98115

George W. Boehlert

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
2570 Dole St.
Honolulu, HI 96822-2396

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47. Reproduction, maturation, and seed production of cultured species. Proceedings of the Twelfth U.S.-Japan Meeting on Aquaculture, Baton Rouge, Louisiana, October 25-29, 1983. By Carl J. Sindermann (editor). February 1987, iii + 73 p. [13 papers.]
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49. Reproduction, movements, and population dynamics of the southern kingfish, *Menticirrhus americanus,* in the northwestern Gulf of Mexico. By Stephen M. Harding and Mark E. Chittenden, Jr. March 1987, iii + 21 p., 8 tables, 10 figs.
50. Preparation of acetate peels of valves from the ocean quahog, *Arctica islandica,* for age determinations. By John W. Ropes. March 1987, iii + 5 p., 4 figs., 1 table.
51. Status, biology, and ecology of fur seals. Proceedings of an international symposium and workshop, Cambridge, England, 23-27 April 1984. By John P. Croxall and Roger L. Gentry (editors). June 1987, v + 212 p. [14 Species Summaries; 12 Contributed Papers; 5 Rapporteurs' Report; 1 Bibliography.]
52. Limited access alternatives for the Pacific groundfish fishery. By Daniel D. Huppert (editor). May 1987, iii + 45 p. [8 papers.]
53. Ecology of east Florida sea turtles. Proceedings of the Cape Canaveral, Florida, sea turtle workshop, Miami, Florida, February 26-27, 1985. By Wayne N. Witzell (convener and editor). May 1987, iii + 80 p. [11 papers.]
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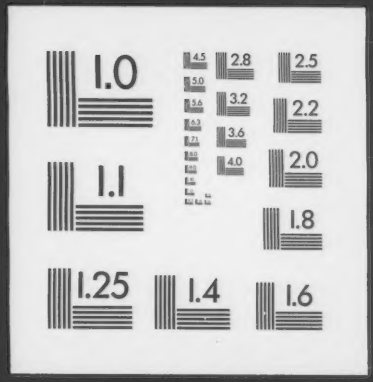
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